# Accumulation of nutrients and biomass during primairy succession and the effect of a shifting allocation pattern on a vegetation

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Accumulation of nutrients and biomass during primairy succession and the effect of a shifting allocation pattern on a vegetation.

Thesis

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The conclusions, only supported by short-term research, are mostly of temporary nature and are on account of the author.

ABSTRACT

We investigated the changes in stand structure, nutrient distribution and various soil factors during the transition from herbaceous to forest vegetation in two successional sequences on the island of Schiermonnikoog.

A previous study indicated nitrogen to be an important limiting factor during the early stages of these successional series (Olff *et al*, submitted). Phosphorus limitation is likely to occur in (more) later stages of succession (Walker & Syers, 1976, Vitousek & Walker, 1987). Although we found a dramatically increasing C/P ratio in the soil along both sequences, we do not yet have further evidence for the occurrence of phosphorus limitation. The nitrogen fixing shrub *Hippophae rhamnoides* is likely to have a strong influence on the accumulation speed of nitrogen in the dune sequence.

During primary succession an increasing nutrient availability causes a shift in the allocation pattern of plants (Tilman, 1988). A higher proportion of the production will be allocated to plant organs with a lower maintenance requirement. We discuss a model dealing with changes in biomass of several stand compartments caused by a change in resource availability. We compared the changes in biomass and nutrient contents of several compartments during primary succession from bare soil to plain- or dune forest with the trends resulting from the model. We suggest two causes of the increase in biomass, the increasing productivity which is the result of a decreasing relative allocation to the root system and a decreasing specific respiration for the whole vegetation.

For both sequences the maximum amount of root per square meter was found in the 28 year old stage. This indicates - according to the model - a shift in allocation from plant organs with a high maintenance to plant organs with low maintenance driven by an increased nutrient availability.

Ever since ecologists started studying the mechanisms of succession chronosequences have been very useful for describing the course of succession. Chronosequences enable the researcher to study different stages of succession at the same time. Shifts in competitive ability during succession can be studied, and the effects of the removal of the limiting factor(s) causing the succession can be tested in experiments (i.e. Olff *et al*, submitted).

Primary succession starts when bare soil is formed after sand dune formation, the retreat of glaciers, heavy erosion or volcanic eruptions. Because usually all mineral elements required by plants occur in the parent material except nitrogen (Jenny, 1980), primary succession is often facilitated by the accumulation of nitrogen in the system. Chronosequences found at Glacier Bay in Alaska (Crocker & Major, 1955, Lawrence, 1979), the Lake Michigan sand dunes (Olsen, 1958) or the beach plain at Schiermonnikoog (Olff *et al*, submitted) showed a change in species composition which was accompanied by a change in the availability of nitrogen relative to light.

At the onset of succession in a system like a bare sand dune the elemental inputs through precipitation will be more or less equalled by elemental loss through hydrological outputs. The bare sand does not have any means of conserving nutrients like nitrogen. When plants begin to colonize the system they will build up several biomass pools which will act as a sink for nitrogen. As long as these compartments continue to increase, nitrogen will be stored and the outputs from the system will be less than the inputs (Vitousek & Reiners, 1975). There is a maximum amount of biomass that can be produced, however (Odum, 1969, Ågren, 1985). This maximum is imposed by the amount of solar energy. If a certain biomass compartment suffers losses, which is the case for most compartments in real nature, it cannot increase indefinitely. As a consequence a steady state may be reached when the production is equal to the loss from the compartment. When the storage capacity approaches a steady state, the nutrient losses from these compartments will become equal to their uptake and the output from the system will become equal to the uptake of the system.

Turnover of biomass compartments is not a universal characteristic of ecosystems. In ecosystems without turnover, increasing nutrient contents will not result in increasing productivity. An example of such a system is a bog. Due to the very low decomposition rate of peat almost no turnover of this

biomass compartment occurs, which therefore becomes a major sink of nutrients, trapping the system at a very low productive state. In most ecosystems however the accumulated biomass will be degraded by herbivores and decomposers (Reiners, 1981). This will cause a release of nutrients stored in these compartments, which may become available for plant uptake. With the accumulation of nutrients during primairy succession, the nutrient supply will shift from precipitation in the early successional stage to recycling within the system in the mature successional stage.

Tilman (1988, 1990) suggested an approach to succession in which plants face certain tradeoffs in allocating carbon to different plants parts, in response to environmental constraints. Allocation to a particular plant part or function will reduce the proportional allocation to other plant parts or functions. This way a plant can maximize its net production. A shift in relative importance from one constraint to another will cause a change in the allocation pattern favoured by competition. As a consequence, changes in stand structure and biomass should be expected.

Plants have to face a tradeoff in allocating carbon to roots or to above-ground structures. Species living under severe nutrient limitations often have a low shoot/root ratio compared with species living in a more nutrient-rich environment. A high proportion of the photosynthesised carbon will be allocated to photosynthetically inactive organs. This causes an increase in the plant compensation point for light and a decrease in the degree to which light can be reduced (Huisman & Weissing, unpublished manuscript). This implies a low gross productivity typical for nutrient poor soils. When we move towards a nutrient-rich environment the proportion of carbon that has to be allocated to the root system decreases. The proportional allocation to photosynthetically inactive plant parts decreases and thus the gross productivity increases. During succession the total amounts of both root biomass and shoot biomass are functions of an increasing shoot/root ratio and an increasing production. In the following section we will discuss these phenomena with a simple model in which we explore the changes in biomass compartmentation caused by a change in resource availability.

The remaining part of this work reports on the changes in stand structure and nutrient distribution during the transition from herbaceous to forest vegetation in two successional sequences on the island of Schiermonnikoog. Combining the data presented in this paper with the data collected by Olff et al (submitted) we can investigate the changes in species composition, biomass

and nutrient distribution on sites with a surface age of 12, 20, 28, 100 and 200 year. Thereby we will be able to investigate changes in biomass and nutrient contents of several compartments during primary succession from bare soil to forest. We will compare these data with the model predictions which will be presented below. In addition, we also investigated a number of other soil factors in order to examine the possibility of other soil factors besides nitrogen determining the course of succession.

METHODS

The effect of a shift in allocation on a vegetation; a theoretical approach.

Let us simplify a stand of higher plants to a system of three biomass compartments. All tissues which are photosynthetically active are gathered in a *leaf compartment*. All tissues which are active in capturing the limiting soil resource are gathered in a *root compartment*. This does not include all underground parts of a plant. Storage organs, for example, are not included in this compartment. All other plant tissues, for instance reproductive organs and stemwood, are gathered in the third compartment, which will be referred to as the wood compartment, since wood will be the largest component.

Before we discuss the relationships between the compartments, we will make a few assumptions.

Assumption 1: A plant, and in turn a whole stand of higher plants, tends to maximize its allocation to nonproductive parts, because such plants often have the greatest resources with which to reproduce and compete for additional space (Givnish, 1988). Non-productive parts are defined here as the plant organs that are not involved actively in the capturing and fixation of energy or the production of new biomass.

Assumption 2: Given a successional stage, the soil resource availability R is constant over time. Different stages may of course have different resource availabilities.

Assumption 3: The Specific Resource Activity (*SRA*) of the roots, which is the amount of resource R taken up per unit root biomass in a unit of time, is an increasing function of the resource availability in the soil during that

period of time, and will reach the maximum specific resource activity SRA_{max} asymptotically. In this model we will use the Michaelis-Menten type of function:

$$SRA = SRA_{max} \frac{R}{K_R + R} \tag{1}$$

where K_R is the half saturation constant for resource R.

Assumption 4: All three compartments suffer losses due to maintenance requirements and death of individual plants. These losses are assumed to be constant per unit compartment biomass and are therefore called specific maintenance requirement SMR.

Assumption 5: The ratio γ of carbon and resource in this requirement is fixed and does not have to be the same as the carbon-resource ratio in the tissue itself. A part of the carbon needed is respirated and not incorporated into newly formed biomass.

The model presented below calculates the biomass of the three compartments in equilibrium for several resource availabilities. In a stable situation the biomass production of the stand equals the turnover of the stand.

Let us look at a stand which consists of BL foliage, BR roots and BS wood. The carbon production of the foliage compartment (C) is a function of light availability, following Monsi & Saeki (1953):

$$C = \frac{P_{max}}{k} \ln\left(\frac{P_{max} + \alpha I_o}{P_{max} + \alpha I_o e^{-k\,BL}} \right) \tag{2}$$

in which P_{max} is the maximal photosynthesis per gram biomass, I_o is the incoming radiation per m^2, k is the light extinction coefficient over leaf biomass and α is a constant.

A certain amount of resource has to be taken up to get a constant resource-carbon ratio γ in the photosynthetically fixed biomass. If a plant is considered to be an optimal forager (Gleeson & Tilman, 1992), the amount of root biomass BR, needed to meet the nutrient demand, depends on the specific resource activity SRA of the roots:

$$BR = \frac{C\gamma}{SRA} \tag{3}$$

Both the foliage biomass and the root biomass require a certain amount of production to compensate for their losses. The amount of production that is left (C_s) will be allocated to the wood compartment. This means that the amount of wood is a function of C_s:

$$BS = \frac{C_s}{SMR_s} = \frac{C - (BL \cdot SMR_L + BR \cdot SMR_R)}{SMR_s} \qquad (4)$$

In order to study the dynamics of this system, it is useful to start with a few additional simplifications. Later onwards, these assumptions are relaxed. Let us equal the specific losses from each compartment, so that $SMR_L = SMR_R = SMR_s$, and look at the equilibrium compartment sizes at different resource availabilities. When the amount of foliage is fixed, we can see a shift from root biomass to stem biomass with an increasing resource availability (fig. 1A). The total amount of biomass which can be maintained remains the same. At the point P the carbon requirement of the root- and leaf biomass is larger than the productivity, and an equilibrium does not exist.

If the turnover of the stem biomass is lowered, figure 1A changes to figure 1B. We can see an increase in the biomass of the whole stand with an increase in the resource availability. This increase is caused by the difference in the specific maintenance of the root compartment and the wood compartment. If vegetation allocates more to a compartment with a lower maintenance requirement, it will be able to meet the maintenance of more biomass altogether.

Until now we have considered a system in which the leaf biomass is kept constant with an increase in resource availability. This is not the case during succession. At a certain resource availability a plant will maximize its allocation to stem biomass, by means of reducing light to the light compensation point. This is the point on a light gradient at which specific carbon uptake of productive tissue equals specific carbon losses. If light is reduced further, part of the leaf biomass will not be productive but rather, require carbon from biomass higher in the light gradient. This reduces the net carbon gain of the leaves. Huisman & Weissing (unpublished manuscript) defined two compensation points, the leaf compensation point and the plant compensation point. The *leaf compensation point* (or instantaneous compensation point sensu Givnish, 1988) corresponds to the light intensity at which specific leaf carbon losses are compensated by specific leaf carbon uptake. The *plant compensation point* (or ecological compensation point sensu Givnish, 1988) is defined by the light intensity at which specific leaf carbon losses

are compensated by the part of the carbon uptake which is kept in the leaves. Reducing light to the leaf compensation point maximizes the allocation to the remaining part of the plant. Reducing light to the plant compensation point maximizes the net carbon gain of a plant. The plant compensation point occurs at higher light intensities than the leaf compensation point. In this model we will reduce light to a *leaf-root compensation point*, defined as the light intensity at which the specific carbon uptake of the combined leaf-root system equals its losses. This point occurs between the leaf compensation point and the plant compensation point. In this way we maximize the allocation to plant parts which are not involved in the capturing and fixation of energy, for instance wood material or seeds.

Since the amount of rootmass is a function of the carbon gain by the leaf, we will have to find the amount of leafmass at which C_S is maximal, in other words where $\delta C_S/\delta BL = 0$. According to appendix A this yields:

$$BL = -\ln\left(\frac{P_{max}}{\alpha I_o \left(\dfrac{G\, P_{max}}{SMR_L} - 1 \right)} \right)/k \qquad (5)$$

where

$$G = \frac{1 - SMR\gamma}{SRA} .$$

With this equation we can calculate the leaf biomass at which the productivity of the leaf-root system is maximal, and from this figure the root and wood biomass, for every resource availability R.

The effect of increasing R on the distribution of biomass is shown in figure 1C. An increased allocation to the leaf compartment causes a decrease of the leaf compensation point. The total amount of leafmass increases leading to a higher gross production, and as a result the amount of wood that can be maintained increases. The amount of both leaf- and wood biomass increase to a maximum at $R=\infty$. A maximum in the amount of rootmass can be found at low R availability. This is caused by an increasing total biomass and a decreasing rootbiomass/totalbiomass ratio. Figure 1D shows the relative amount of leaf, wood and root for every R. A decreased proportion of root can be found, and an increased proportion of wood. The proportion of leaf reveals a maximum at intermediate levels of resource availability.

The growth of biomass starts at point P (fig. 1C), when the *SRA* of the roots is higher than the turnover of the resource ($SMR_R * \gamma$). This can be derived from equation 2 in the appendix. If the term between brackets becomes

negative, then *Cs* becomes negative, no matter what leafbiomass is used.

When comparing the trends suggested by the model with the data, we must keep in mind, that the axis of the figures with the data represents a time axis, whereas the model predictions are formulated in terms of nitrogen availability. It is unlikely that the increase of nitrogen availability is a linear function of time. In the most simple situation the nitrogen availability will be lowest at the onset of succession and will increase with a decreasing increment, thereby approaching a kind of steady state.

The validity of using this model for vegetation succession depends strongly on whether succession can be considered as a series of equilibria, resulting from a slowly changing nutrient availability (Tilman, 1988). It is uncertain whether the deviations from the equilibrium compartment sizes can be considered negligible. This can be illustrated by an example: A plant species which dominates a specific stand might be able to suppress the settling of another plant species for a long time. When the dominant species has a certain allocation pattern which is suboptimal for the current nutrient availability, it might be able to cause deviations from equilibrium compartment sizes until it is finally replaced by a species better adapted to the local situation.

The model presented above has a major simplification. It assumes that the parameters $P_{\underline{max}}$, α, $SRA_{\underline{max}}$, $K_{\underline{r}}$, k, γ and the SMR's are independent of resource availability. A change in species composition will probably cause a change in one or more of these parameters. As a consequence an increase in R availability will not necessarily have to lead to a change in the sizes of the compartments in this model. If, however, the trends predicted by this model can be found in real nature, this model suggest a possible explaination.

Site description

The study sites were located on the Wadden Sea island of Schiermonnikoog, The Netherlands (ref 53°29' N, 6°12' E). At the eastern part of the island new soil is being formed continuously, as the island "moves" to the east. On the island several successional stages can be found, ranging from bare sand on the beach to forest at the oldest parts. Apart from the successional stage, the species composition of the vegetation on the island is also determined by soil elevation , which is related to salinity, flooding frequency and soil moisture. Olff et al (submitted) distinguished three early successional sequences; for the wet plain, for the intermediate dune slopes and for the dry

dunes. To extend their data set to older successional stages, four additional sites were located; two in larger dune slacks as an extension of the plain sequence, two on the dunes as an extension of the dune sequence (table 1).

The Johannesbos site lies in a big dune slack of approximately 90-100 year old, situated on the north of the island (fig. 2: site A). The slack consisted of young *Betula* thickets mixed with patches of *Phragmites australis*. The Phragmites patches are sometimes mown in winter. A 10m x 30m quadrat was established, in order to analyze the biomass compartmentation. The vegetation of this quadrat was merely composed of young *Betula pubescence* trees, with the exception of one living *Hippophae rhamnoïdes* shrub and several dead specimens of this species. No shrub layer was present. The herb layer consisted mainly of *Calamagrostis epigejos* and *Phragmites australis*.

The Berkenbos site lies in a dune slack of approximately 200 year old, situated in the middle of the island (fig. 2: site B). A 30m x 30m quadrat was positioned in an area with a well developed *Betula pubescence* stand for comparison with the younger *Betula* stand at the Johannesbos. The understorey consisted of *Alnus glutinosa*, from which a few had reached the upper canopy, and a few *Salix cinerea*. The herb layer consisted of *Calamagrostis epigejos*, *Agrostis stolonifera* and *Holcus lanatus*.

The Kobbebos site was situated on the Kobbeduinen, a dune system located on the eastern part of the island (fig. 2: site C). It was formed approximately 90-100 years ago. The vegetation was quite diverse, mostly the dune tops and the little dune slacks were covered by more or less dense *Hippophae rhamnoides* shrubs, the slopes were covered by *Sambucus nigra*. The herb layer underneath the *Hippophae* was composed of *Calamagrostis epigejos* and *Chamerion angustifolium*. The herb layer underneath the *Sambucus* was composed of *Urtica dioca*. A 30m x 30m quadrat was situated containing 3/4 of a dune ridge.

The Kooibos site was located on top of the Kooiduinen, which is a dune ridge approximately 200 year old (fig. 2: site D). A 30m x 40m quadrat was located covering 3/4 of the top of the dune. The slopes of the dune featured no mature trees, probably due to recent human interference or grazing by cattle. The quadrat was occupied by *Betula pubesence* in the lower part and *Prunus serotina* and *Acer pseudoplatanus* in the upper part. The understorey consisted only of a few *Sambucus* trees. The herb layer was composed of *Calamagrostis epigejos* and *Agrostis stolonifera* underneath the *Betula* trees,

and of *Urtica dioica* and seedlings of *Prunus*, *Acer* and *Sambucus* underneath the *Prunus* and *Acer* trees. On the top of the dune a few *Hippophae* shrubs could be found.

The dune sites were not homogeneous in composition probably due to the heterogeneity of the soil. A number of plant communities could be distinguished at the Kobbebos site, among which a *Sambucus* dominated vegetation and a *Hippophae* dominated vegetation were the most abundant. The vegetation on both sites appeared to be very dependent on the elevation and orientation of the dunes. Therefore, the size of the **sampled** quadrats was most likely too small to get a representative view of the total species composition of the dunes.

Biomass and nutrient concentrations

Diameter at breast height (DBH) and tree height of all tree and shrub species within the quadrat with the exception of *Salix repens* were measured. DBH was measured only if the tree was large enough, otherwise the diameter below the lowest branch was measured. The location of the stem and the periphery of the crown were drawn on a map, from which the coverage of every individual tree was calculated using a G.I.S. system. In the Berkenbos and Kooibos site, two storeys of tree/shrub species could be distinguished. For these sites maps of the understorey were also made.

The biomass of the tree stratum was estimated using regression equations for the five most abundant trees within the quadrats, which were *Betula*, *Alnus*, *Sambucus*, *Prunus* and *Acer*. Trees were harvested outside of the quadrats and DBH, tree height, stem+branch fresh weight and leaf fresh weight measured. The leaves were dried at 70° C for at least 24 hours and weighted again. Samples of wood were weighted, dried at 70° C for at least 72 hours, and weighted again, from which the water content of wood material was estimated. From this figure stem dry weight was calculated. The stem dry weight of the trees within the quadrats was estimated from the DBH, combined with tree height (optionally). From the stem dry weight the leaf dry weight was estimated (Table 2). The regression equations were based on trees ranging in DBH from 0.4 to approximately 8 cm. When using the equations for estimating the biomass of trees with a diameter higher than 8 cm the error included in the estimations will become very large.

For *Hippophae* the DBH-biomass relation measured by Olff et al (submitted)

was used. We measured the diameter at the bottom of the stem, following the method used by Olff et al. The proportion leaf biomass, which was not included by Olff et al, was estimated to be 5 percent.

The herb layer was sampled by harvesting 3 subquadrats of 0.4m x 0.4m randomly distributed within each site. The above-ground biomass was sorted out with respect to species and dead organic matter, dried at 70° C for at least 72 hours and weighted.

Roots were collected by taking two soil cores per subquadrat (20 cm deep 38.5 cm² area). The roots were rinsed under a fine water spray. Roots with a diameter of more than two millimetres where separated from the fine roots, and all fractions were dried at 70° C for at least 72 hours and weighted.

Dried samples from leaves and stems, collected when harvesting the trees used for making the regression equation, leaves harvested in the autumn, the shoots of the herb species and both the root fractions were pooled and mixed per species and 2 subsamples were gathered for each sample. These subsamples were analyzed for total N (destruction with salicyl-sulphur + Se + thiosulphate, NH_3-colorimetrisch) and total P (destruction with Fleischmann acid).

Soil measurements

At all sites the soil consisted of an organic layer on top of a sandy underground. At the Johannesbos and Berkenbos sites, the organic layer was peat-like and mostly very wet. The Kobbebos and Kooibos sites had a organic layer which consisted of much further decomposed organic matter and was less wet than the sites situated in the slack.

The thickness of the organic layer was measured at ten randomly chosen points in each subquadrat. Samples were taken from the organic and the mineral layer by pooling the organic or mineral parts from several cores of 20 cm depth sampled at each subquadrat. This resulted in three organic layer samples and three mineral layer samples per site. These samples were analyzed for NaCl (water solution), $CaCO_3$ (titration with 1 N HCl), pH (KCl, 1 volume soil with 5 volumes 1 N KCl), organic matter content (loss on ignition at 550 °C), total carbon (Carmhomat analyzer with correction for $CaCO_3$), total nitrogen (destruction with phenole-H_2SO_4 +Se, NH_3 colorimetric) and total phosphorus (destruction with Fleischmann acid). The moisture content and bulk density

(volume per weight) were measured at 0-5 cm and 15-20 cm depth, using 100 ml pF-rings. The N and P content in the organic layer (g/m^2) were estimated for all sites using the bulk density, average thickness and N- or P-concentration of the organic matter.

The effects of successional stage (12, 20, 28, ±100 and ±200 year) and elevation (plain and dune) and/or layer type (organic, mineral) were statistically tested using analysis of variance with polynomial contrasts for the successional stages. The dependent variable was log-transformed prior to the analysis if this improved the homogeneity of the variances (as tested by Cochran's C test).

RESULTS

Species dynamics

The dominant species in the first years of succession on the plain were *Glaux maritima* and *Agrostis stolonifera*. In the second investigated stage, 20 years after soil formation, *Juncus gerardii* was dominant. In the 28 year old stage *Juncus gerardii* still was the dominant species, but *Phragmites australis* and *Scirpus maritimus* increased in abundance. In the Johannesbos *Betula pubescense* was the dominant species. In the Oldest stage *Alnus glutinosa* had started to invade the forest, but *Betula* was still the most abundant plant species.

The dune sequences started with *Ammophila arenaria*, the later stages were dominated by *Hippophae rhamnoides*. In the 100 year old stage *Sambucus nigra* became the most important species, replacing *Hippophae*. *Betula* and *Prunus serotina* were the most dominant in the oldest stage, while *Acer psuedoplatanus* will probably be the next dominant species. *Chamerion angustifolium* attributed considerably to the biomass in the third and the fourth stage. *Urtica dioica* managed to build up a large amount of biomass underneath the *Sambucus* thickets at the fourth stage. An extensive investigation of the species dynamics of the first three stages is given by Olff et al (submitted).

Biomass and nutrient concentrations

Biomass of above-ground plant components accumulated slowly in the first

stages of succession, then rapidly during the transition from herbaceous- to shrub and forest vegetation, and slowed down between the forth and the last stage, for both the plain and the dune sequence (fig. 3 A). The amount of green plant parts increased to a maximimum at the third stage at both the sequences, but then decreased considerably (fig. 3 B). The biomass of the herb layer remained relatively constant during the plain sequence over the last two stages, at the last stage of the dune sequence the herb layer declined to almost zero. The absolute amount of roots increased to a maximum in the early stages of succession, and then decreased again in the older stages of both sequences (fig. 3 C). The rootbiomass was always larger in the plain sequence. Both the shoot/root and the leaf/root ratios are given in figure 3 D. In literature the shoot/root ratio is used as a measure for the allocation pattern of a plant (Olff et al, 1990). The shoot/root ratio however gives a false impression of the allocation to root or shoot when used to compare plants with permanent structures, in which biomass accumulates, with plants that do not have permanent structures. A better measure would be the leaf/root ratio in which leaf stands for all non-permanent above-ground plant structures. In this study we did not separate leaves from stems for herbaceous species, and both measures are given. The leaf/root ratio increased to a maximum at the plain sequence. The shoot/root ratio showed a maximum at the third stage. The leaf/root ratio and the shoot/root ratio at the dune sequence showed a much more irregular pattern, probably due to large variations in the amount of leaf.

Nutrient content of the vegetation

Both sequences showed an increase of the above-ground total nitrogen content (g/m^2), which seemed to be levelling off (fig. 4 A,B). The dune sequence showed a very strong increase in nitrogen, potassium and phosphorus content between the 20 and 28 year old stages (fig. 4), probably caused by the fast growth of the nitrogen fixing shrub *Hippophae*. The nitrogen content of the wood compartment is relatively low. The above-ground potassium content at the plain sequence showed an increase only from the 0 to the 20 year old stage, but then remained constant (fig. 4 C). The dune sequence showed a maximum of the potassium and phosphorus content at the 100 year old stage. Both the potassium content and the phosphorus content of the 200 year old stage showed lower values, probably to a large extend due to the lack of a

herbaceous layer. In both sequences the herb layer contained a relative relatively large proportion of the total potassium. The litter layer showed a very low potassium content.

The nutrient content of the roots, separated in a fine root class and a rhizomes/thick root class is given in figure 5. The nitrogen concentration in all the fine roots for both sequences showed a significant increase (family wise error: $p<0.001$). The increase of nitrogen concentration in the rhizomes/thick root - class was only significant for the dune sequence ($F_{1,13}$ = 18.78; $p=0.001$). The potassium content showed a significant decrease in the plain sequence for both root types ($F_{1,13}=70.35$; $p<0.001$). The dune sequence did not show a significant trend in potassium content. Only the phosphorus concentration of the fine roots on the dune sequence showed a significant increasing trend ($F_{1,8}=1057.04$; $p<0.001$).

Soil measurements

Both sequences showed an increase in the thickness of the organic layer from 0 to approximately 10 cm at the 200 year old stage (fig. 8 C). The increase was larger on the plain sequence. The moisture content of the soil was significantly lower at the dune sequence ($F_{1,100}=991$; $p<0.001$, fig. 6 A,B). The upper layer for both sequences showed a significant increase in moisture content ($F_{1,50}=55$; $p<0.001$). The NaCl content at the plain sequence reached a maximum in the early stages of succession (fig. 6 C,D). The last two stages were not inundated with sea water during winter and showed a much lower NaCl content. The dune sequence had only very low NaCl contents. The $CaCO_3$ content of the organic layer was high in the first two stages of succession for both sequences (fig. 6 E,F). In the last three stages the $CaCO_3$ concentrations became very low. In the third stage the mineral layer showed a significant higher $CaCO_3$ content than the organic layer, for both sequences (tested a posteriori with SNK's range test). In the two latest stages the $CaCO_3$ concentration of the (upper) mineral layer has become very low. The pH of the organic layer decreased instantly after soil formation, while the decrease in pH in the mineral layer showed some delay (fig. 6 G,H). This was tested using only the first three stages. The organic layer showed a significant decrease ($F_{1,24}=187$; $p<0.001$), while no significant decrease could be found in the mineral layer.

During succession both sequences showed an increase of nitrogen concen-

tration in the organic layer ($F_{1,20}=242$; $p<0.001$, fig. 7 A). In the mineral layer nitrogen accumulated to a much lesser extend, although the increase was also significant ($F_{1,20}=96$; $p<0.001$, fig. 7 B). The differences between the organic layer and the mineral layer were much less apparent for the P concentration (fig. 7 C,D). There was no significant difference between the two sequences. The P-concentration reached the highest values in the third stage of the plain sequence. A significant part of the variance was described by the second and third order polynomial, indicating the occurrence of a maximum. The P concentration in the organic layer of the dune sequence showed a significant increase ($F_{1,20}=18$; $p=<0.001$). The P-concentration in the mineral layer of the plain sequence showed a significant decrease ($F_{1,20}=38$; $p<0.001$), while the mineral layer in the dune sequence did not have a significant trend. The C/N ratio in the organic layer of the plain sequence showed an increase in both sequences ($F_{1,20}=23$; $p<0.001$, fig. 7 E). The C/N ratio of the mineral layer was variable, with no significant trend occurring ($F_{1,20}=156$; $p<0.001$, fig. 7 F). The C/P ratio in the organic layer increased drastically in both the sequences ($F_{1,20}=72$; $p<0.001$, fig. 7 G). The C/P ratio in the mineral layer also increased, but remained much lower for both sequences, due to a lower C content in the mineral soil (fig. 7 H).

Since the depth of the organic layer varied between successional stages and sequences, the N and P concentration had to be multiplied by the thickness of the organic layer to obtain the total accumulation per unit area (fig. 8). In both sequences there is a significant increase in the N-content of the organic layer ($F_{1,20}=171$; $p<0.001$; fig. 8 A). The accumulation of N in the organic layer was caused both by the increase in the thickness of the organic layer and the increase in the concentration of N in the soil (Fig 7a). The P content seemed to have an maximum in the fourth stage for both sequences (fig. 8 B).

Figure 9 shows the aboveground biomass, nitrogen and phosphorus per square metre of the living biomass, litter and soil organic mater (including fine roots). The contents of the larger below ground roots were not included. The SOM was the largest pool for both biomass, nitrogen and phosphorus.

The percentage retranslocation and the amount of nutrients released with leaf senescence per m² were calculated (fig. 10). *Hippophae* appeared to be a very nutrient efficient species. The species that succeeded this species on the dune sequence, *Sambucus nigra*, appeared to be the most nutrient inefficient. The amount of nitrogen released per m² by *Sambucus* was ten times higher than the amount released by *Hippophae*.

DISCUSSION

In most cases, if not all, succession is accompanied with changes in environmental factors. These factors may have caused the succession, may be the result of succession, or may have no relation with succession. In this study we found a change in water content, NaCl content, lime content, pH, biomass content, phosphorus content and nitrogen content of the soil. In the following part we will discuss the influence of these factors on species replacement and biomass accumulation.

The build up of organic matter on top of the soil probably increased the water retention capacity of the soil. This may have caused the increased water content of the organic layer for both sequences. This increased water content is likely to influence the rate of mineralisation and thus the availability of nutrients. Due to deep drainage and a decreasing influence of the sea the salt and lime content dropped with the aging of the soil. The high NaCl content of the soil in the early stages is likely to suppress plant production. Hydrological loss of NaCl took place rapidly on the early stages of the dune sequence. We found almost no NaCl in the soil at the first site of the dune sequence. Assuming a high NaCl content of the sand due to the sea water influence at the start of the dune formation, the hydrological loss of NaCl must have been very high. The lime content of the organic layer decreased much faster than the lime content of the mineral layer. Organically bound calcium is much more susceptible to leaching then mineral calcium (Truddgill, 1977). The pH decreased along with the lime content of the soil, also showing a lag for the mineral layer in the earlier stages of succession. The colonisation of bare sand by plants started the accumulation of biomass in the soil, called soil organic matter (SOM). Although the accumulation of SOM does not directly influence the plants growing upon the soil, Vitousek and Reiners (1975) supposed that it is the major force driving the succession, because SOM increases the nutrient retention capacity of the soil. This agrees with the results of the present study. Both the nitrogen concentration and the nitrogen content in the organic layer increased in both sequences. Phosphorus did not show such a large increase. There were no inputs of phosphorus other than mineral weathering. Although the inorganic (Ca-bound) phosphorus content of the beach sand is likely to be high, most of it will likely be lost due to

drainage, especially on sites where the pH was found to be very low. Pattern for the partitioning of phosphorus in the soil were given by Walker & Syers (1976), based on extensive chemical fractionation studies of four soil chrono-sequences in New Zealand. They found organically bound phosphorus in the soil increasing with time towards the middle of succession, whereafter it declined. This is in agreement with the observations in this study. The highest phosphorus concentrations in the organic layer of the plain sequence were found in the third stage. The phosphorus concentration of the roots did not reveal a large and consistent decrease. The C/N ratio showed only a small increase compared with the C/P ratio indicating a strong connection between the nitrogen and the biomass pool.

Salt stress, flooding and moisture content were likely to influence succession in the early stages of this succession (Olff et al, submitted). Phosphorus limitation is likely to occur in (more) later stages of succession (Walker & Syers, 1976, Vitousek & Walker, 1987). Although we found a dramatically increasing C/P ratio along both sequences, we do not yet have further evidence for the occurrence of phosphorus limitation.

In both sequences the above-ground biomass increased to approximately 4000 g/m^2 (40 ton/ha), which is relatively low compared to the average above-ground biomass for temperate deciduous forests of 15190 g/m^2 (Cole & Rapp 1981). The amount of SOM reached approximately 5000 g/m^2. This is one fourth of the average amount of mature temperate deciduous forests. Therefore we must not consider the 200 year old sites to be the mature stages of succession.

The dune sequence showed a large increase in biomass and nutrient content between the second and the third stage, compared with the plain sequence. This is probably the result of the appearance of the nitrogen fixing shrub *Hippophae rhamnoides*. The extra input of nitrogen to the soil (Olff et al, submitted) probably increased the mineralisation rate and as a result the SOM content, phosphorus content and nitrogen content of the soil decreased. The increase in availability of nutrients caused an increase of productivity and biomass content. This resulted in a large difference between the SOM and nitrogen content of the plain and the dune sequence at the fourth stage. The short-term effect of the appearance of *Hippophae* was probably an increase in mineralisation which decreased the amount of SOM, while the long-term effect was a faster build up of SOM due to a higher productivity. Nitrogen fixing species are known for their capacity to alter the rate of biomass accumulation and nutrient availability (Vitousek, 1990).

Both sequences showed a maximum in the amount of root in the upper 20 cm of the soil at the 28 year old stage of succession. This is in agreement with the predictions made in the introduction. Like Borman & Sidle on the chronosequence of the Glacier Bay National Park, for practical reasons we did not measure the total underground biomass. We assume that only the roots in the upper 20 cm of the soil will be involved in nitrogen uptake, since the majority of the nitrogen is likely to become available through mineralisation in the organic layer. The peak of root biomass in early succession is a strong indication for the occurrence of a shifting allocation pattern in which less biomass is allocated to the root system. This implies that more carbon can be used for the maintenance of other plant organs.

Since herbs do not show distinct differentiation between tissues with a supporting function and tissues with a productive function it is difficult to get a measure of the increase or decrease of productive tissue. We cannot compare the productive biomass measured in the study with the foliage compartment in the model. A further step would be to measure the amount of chlorophyll or rubisco per square metre.

Odum (1969) presented a series of hypotheses for trends associated with successional development of ecosystems. One of these hypotheses stated that the amount of standing crop biomass supported by the available energy flow increases to a maximum in the mature or climax vegetation. Odum did not propose any mechanisms other than biomass accumulation in a simple system until the production equals the respiration of the biomass which is being build up. The system is based on a build up of biomass in absence of changes in nutrient availability or other factors which usually accompany succession.

With some understanding of the tradeoff mechanisms we can go into much more detail. These mechanisms give plants the opportunity to influence their allocation to organs with different maintenance. The amount of respiration of vegetation is altered in response to the amount of environmental stress the plants have to cope with (Taylor, 1989). A more stressful situation, like nutrient deficiency or high salt concentration, forces plants to invest a large part of the production of photosynthates in plant organs with a high metabolic requirement or a high loss rate. A less stressful situation gives plants the opportunity to invest more in stemwood with a low specific maintenance cost which gives them the opportunity to gain a competitive favourable position for light capture. The model presented above investigates the effects of decreasing allocation to the root system on the amount of

biomass that can be maintained. We found two causes of the increase in biomass, the increasing productivity which is the result of a decreasing relative allocation to the root system and a decreasing specific respiration for the whole vegetation.

There are other mechanisms which can cause a shift from biomass with high maintenance to biomass with low maintenance. A less stressful situation gives plants the opportunity to choose between two strategies: being a fast growing species or a slow growing species. A fast growing species will put much effort in gaining a competitive favourable position with respect to light, by means of building a large quantity of wood with a low quality per unit of produced carbon. A slow growing species temporarily tolerates an unfavourable position by slowly building up a small quantity of wood with a better quality per unit of produced carbon. In the long run this might give two advantages. A slow growing species might live longer and can therefore wait until a favourable situation occurs. A lower specific turnover of wood biomass allows for the maintenance of more biomass allowing a slow growing species to become much higher than a fast growing species. The only disadvantage is that the species has to be able to survive a situation with a low light availability. The amount of allocation per unit of produced carbon to other plant organs, for instance the roots, has to be low (Huisman & Weissing, unpublished manuscript). This slow-growing strategy is therefore only favourable in less stressful situations.

This study emphasises the fundamental difference between a tradeoff in allocation between plant organs within the productive unit, e.g. between roots and leafs, and a tradeoff in allocation between a plant organ within and a plant organ outside of the reproductive unit, e.g. between roots and wood. A tradeoff in allocation between plant organs within the productive unit forces plants to find the *ratio* of allocation between both organs at which the production is maximal. However, when facing a tradeoff in allocation between a plant organ within and a plant organ outside of the reproductive unit, the plant which has the ability to alocate the largest *absolute* amount of biomass to the organ outsite of the productive unit, has the best competitive abilities.

The tradeoff mechanisms do not only apply to higher plants. The effects of higher nutrient availability might also influence the biomass and activity of other types of organisms, e.g. microorganism or herbivores. A decreasing metabolic quotient is also observed for soil microorganisms during succession

(Insam & Haselwandter, 1989). The influence of an increasing nutrient availability and the changes in tradeoffs on microorganisms and the size and structure of food webs in the soil will be a interesting field of study for ecologists in the future.

The mechanisms stated above are not exhaustive nor exclusive. There may be more mechanisms involved which influence the increase of the biomass/energy ratio. The mechanisms described above are also likely to occur simultaneously. Investigations about their relative importance have yet to be made.

CONCLUSIONS

Phosphorus limitation is likely to occur in later stages of succession (Walker & Syers, 1976, Vitousek & Walker, 1987). Although we found a dramatically increasing C/P ratio along both sequences, we do not yet have further evidence for the occurrence of phosphorus limitation.

The nitrogen fixing shrub *Hippophae rhamnoides* is likely to have a strong influence on the accumulation speed of nitrogen in the dune sequence. The maximum in the amount of root per square meter in the 28 year old stage for both sequences gives an indication for the occurrence of a shift in allocation from plant organs with a high maintenance to plant organs with low maintenance caused by an increase in the amount of available nitrogen. Further investigations are needed to gain more insight in the effects of a shift in tradeoffs on the net ecosystem production and the biomass/energy flux ratio along successional sequences.

ACKNOWLEDGMENTS

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Allocation to roots is given by the total carbon production minus de maintenance of the leaves and the roots:

$$C_s = C - \frac{SMR_R\gamma}{SRA}C - SMR_L BL \tag{A1}$$

$$C_s = \left(1 - \frac{SMR_R\gamma}{SRA}\right)C - SMR_L BL \tag{A2}$$

We can substitute G for the group of constants $(1-SMR_R\gamma/SRA)$, and replace (2) for C. In order to find for which leaf biomass, BL, the stem biomass, BS, is maximal, we will have to differentiate C_s over BL:

$$\frac{dC_s}{dBL} = G\frac{P_{max}\alpha I_o e^{-k\,BL}}{P_{max}+\alpha I_o e^{-k\,BL}} - SMR_L \tag{A3}$$

Maximizing C_s implies $\delta C_s/\delta BL=0$, which yields

$$(P_{max}+\alpha I_o e^{-k\,BL})\ SMR_L = GP_{max}\alpha I_o e^{-k\,BL} \tag{A4}$$

$$\alpha I_o e^{-k\,BL}SMR_L+P_{max}\ SMR_L = G\alpha P_{max}I_o e^{-k\,BL} \tag{A5}$$

$$P_{MAX}SMR_L = (GP_{max}-SMR_L)\,\alpha I_o e^{-k\,BL} \tag{A6}$$

$$e^{-k\,BL} = \frac{P_{max}SMR_L}{\alpha I_o(G\,P_{max}-SMR_L)} = \frac{P_{max}}{\alpha I_o\left(\dfrac{G\,P_{max}}{SMR_L}-1\right)} \tag{A7}$$

$$BL = -\ln\left(\frac{P_{max}}{\alpha I_o\left(\dfrac{G\,P_{max}}{SMR_L}-1\right)}\right)/k \tag{A8}$$

which is the equation we need.

CAPTIONS TO THE FIGURES :

Fig. 1: Changes in equilibrium compartment sizes caused by an increase of the availability of resource R for a very simple model (A) to a more complex one (C). For explaination read the introduction.

Fig. 2: The Locations of the study sites on the island of Schiermonnikoog. A: Het Johannesbos, B: Het Berkenbos, C: Het Kobbebos, D: Het Kooibos.

Fig. 3: Distribution of Areal biomass (A,B), Productive plant parts (C,D), Root biomass in the upper 20 cm of the soil (E,F), shoot/root and leaf/root ratio (G,H) during primary succession for both the plain and the dune chronosequence. The trianges in graph G and H stand for the shoot/root ratio, the circles stand for the leaf/root ratio. Foliage denotes only the foliage of the trees standing on the site. The total areal herb biomass in gathered in the Herbs compartment. The trunks of trees and roots bigger than 1 cm were omitted.

Fig. 4: Nitrogen content (A,B), Potassium content (C,D) and phophorus content (E,F) of the above-ground biomass during primary succession for both the plain and the dune chronosequence. Foliage denotes only the foliage of the trees standing on the site. The total areal herb biomass in gathered in the Herbs compartment. The root biomass is the amount of roots in the upper 20 cm of the soil. The trunks of trees and roots bigger than 1 cm were omitted.

Fig. 5: Nitrogen concentration (A,B), Potassium concentration (C,D) and phophorus concentration (E,F) of roots in the upper 20 cm of the soil during primary succession for both the plain and the dune chronosequence. Fine root denote roots smaller than 2 cm diameter, rhizomes denote the rhizomes and the roots bigger than 2 cm diameter.

Fig. 6: Changes in moisture content, NaCl content, lime content and pH (KCl) in the organic and mineral layer during primary succession for both the plain and the dune sequence.

Fig. 7: Changes in N concentration (A,B), P concentration (C,D), C/N ratio (E,F) and C/P ratio (G,H) in the organic and mineral layer during primary succession for both the plain and the dune sequence.

Fig. 8: Accumulation in the organic layer of nitrogen N (O), phosphorus P (□) (A,B) and Carbon C (◇) (C,D) in grams per square metre during primary succession for both the plain and the dune sequence. The last two figures also contain the thickness of the organic layer L (▽) in centimetres.

Fig. 9: Biomass content (A,B), nitrogen content (A,B) and phosphorus content (A,B) of the total above-ground living biomass, litter and soil organic matter (SOM) compartments during primary succession for both the plain and the dune sequence.

Fig. 10: Retranslocation of nitrogen, potassium and phosphorus (A) and Nutrient losses per square meter (B) of the main phanerophyte species during autumn leaf senescence. BETULPUB: *Betula Pubescence*; ALNUSGLU: *Alnus glutinosa*; HIPPORHA: *Hippophae rhamnoides*; SAMBUNIG: *Sambucus nigra*; PRUNUSER: *Prunus serotina*; ACER PSU: *Acer psuedoplatanus*.

Table 1: Stand and surface age characteristics and the number of trees per species of the sampled sites along the plain and dune chronosequences.

Site characteristics :	Johannesbos	Berkenbos	Kobbebos	Kooibos
age of the soil (yr)	±100	±200	±100	+200
sequence	plain	plain	dunes	dunes
stand height (m)	5	11	4	9
trees per ha	8300	5866	4200	3283
Trees per species :				
Betula pubescens	248	80	-	132
Alnus glutinosa	-	445	-	-
Sambucus nigra	-	-	188	107
Salix cinerea	-	3	-	-
Hippophae rhamnoides	-	-	119	18
Crataegus monogyna	-	-	3	12
Sorbus aucuparia	-	-	6	2
Prunus serotina	-	-	4	72
Acer psuedoplatanus	-	-	-	49
Rubus caesius	-	-	49	-
Ribis nigrum	-	-	9	-
Total :	249 (300m^2)	528 (900m^2)	378 (900m^2)	394 (1200m^2)

Table 2: Biomass equation developed for estimating the aboveground tree biomass on the last two sites for both sequences.

Biomass equations developed for estimating stem biomass
$$Stembiomass = C \cdot Diameter^A \cdot Height^B$$

Species	C	A	B	n	R^2
Betula	22.7	2.58		8	0.997
Alnus	32.4	2.68		8	0.994
Sambucus	33.2	2.16	0.53	14	0.992
Prunus	48.1	2.33		10	0.989
Acer	30.4	1.99	0.77	11	0.994

Biomass equations develped for estimating foliage biomass
$$Foliagebiomass = C \cdot Stembiomass^A$$

Species	C	A	n	R^2
Betula	0.15	0.90	8	0.881
Alnus	0.62	0.76	8	0.997
Sambucus	0.91	0.72	14	0.950
Prunus	1.72	0.68	10	0.960
Acer	0.98	0.80	11	0.832

fig 1

beach

plain

dunes

(A)

(B)

(C)

(D)

salt marsh

beach

polder

beach

fig 2

PLAIN SEQUENCE

DUNE SEQUENCE

A Foliage Wood Herbs Litter

B Foliage Wood Herbs Litter

C Herbs Foliage

D Foliage Herbs

E

F

G

H
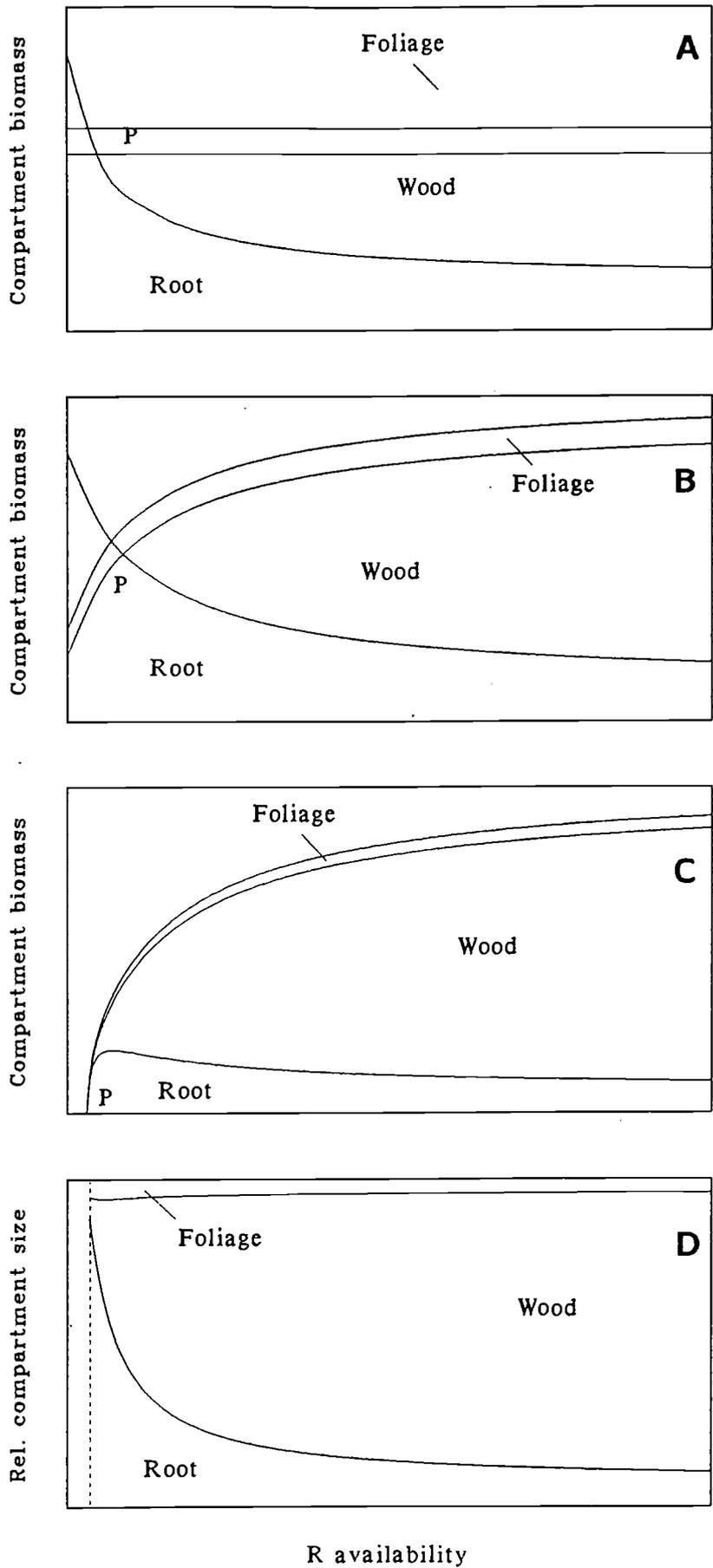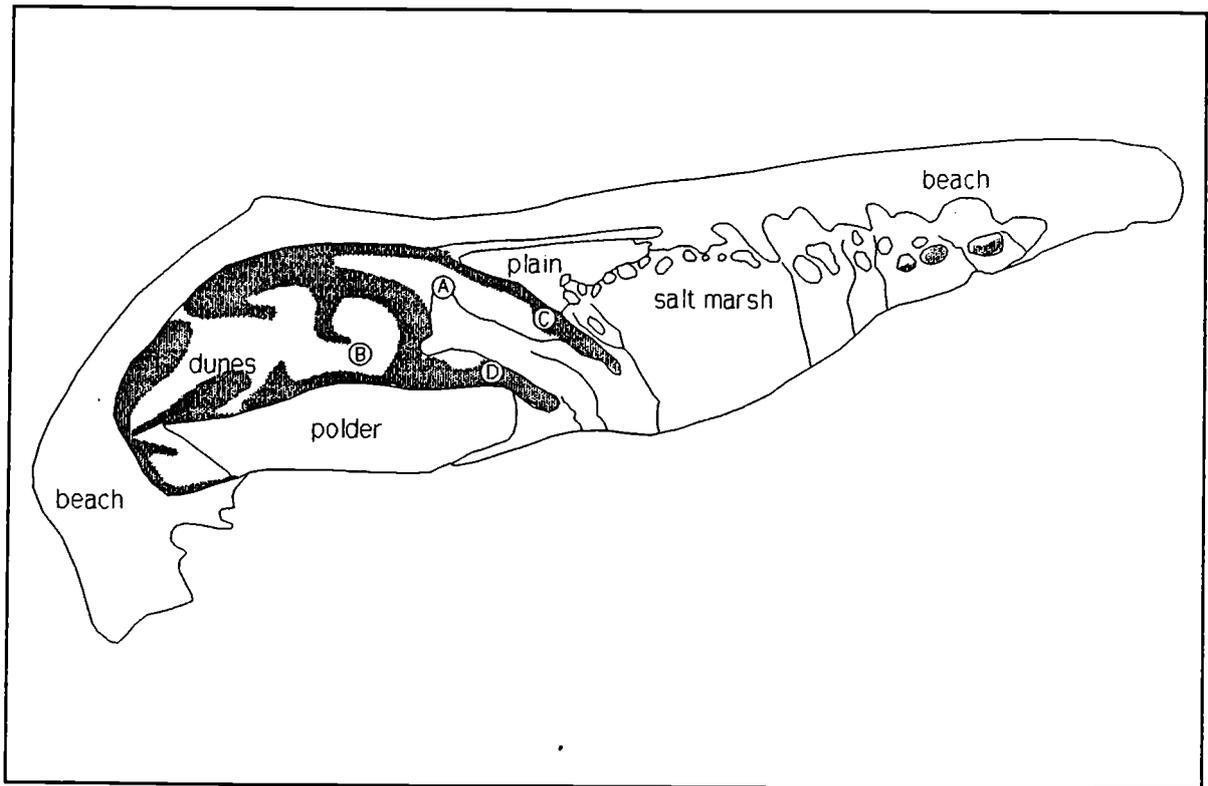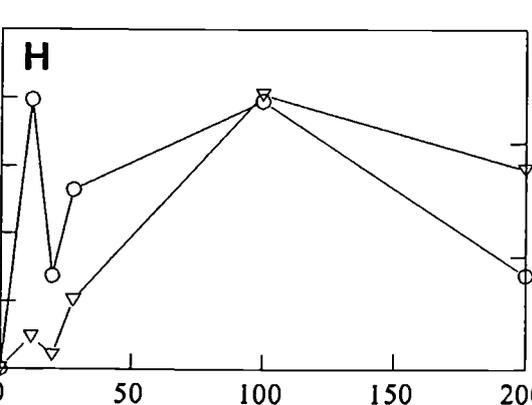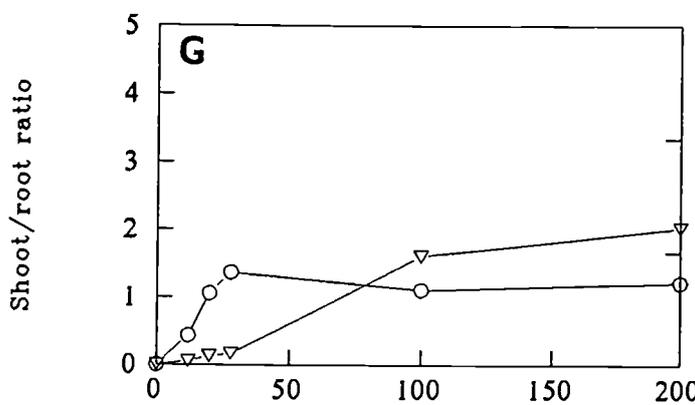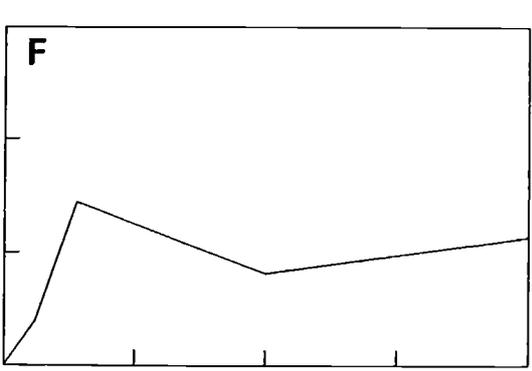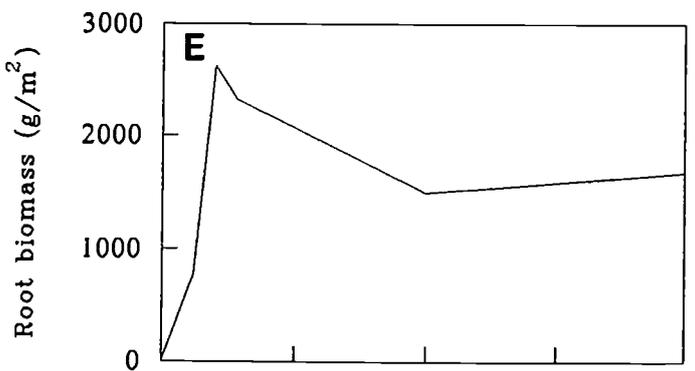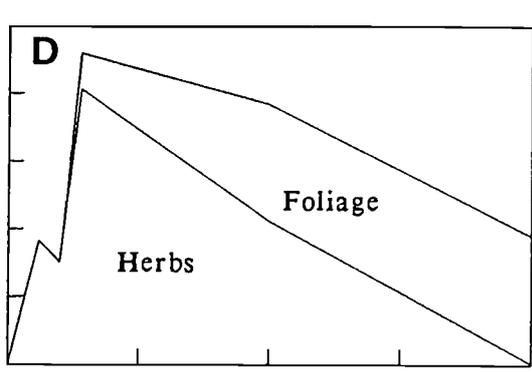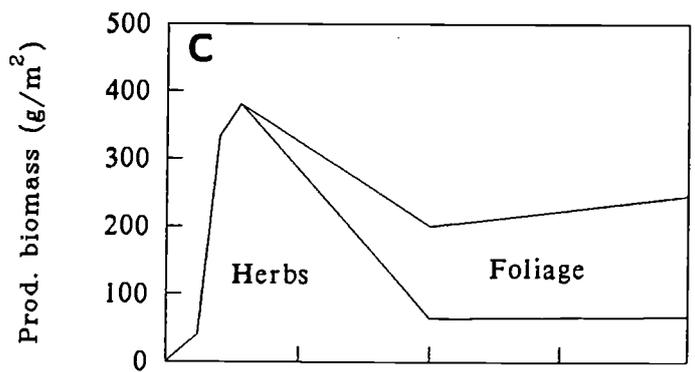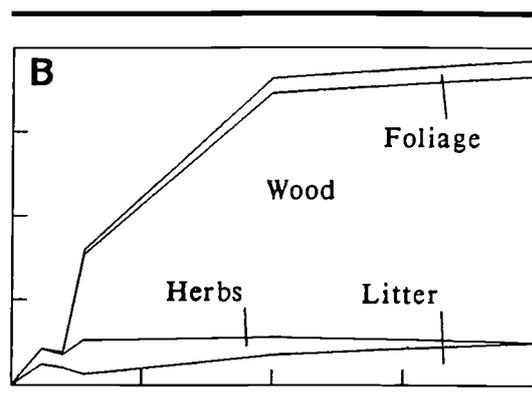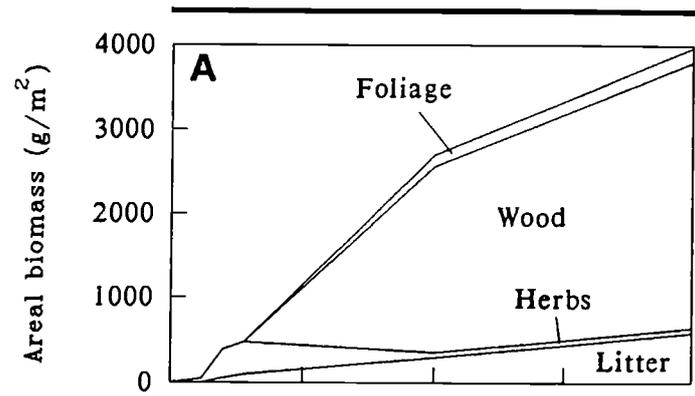
Soil-surface age (years)

fig3

PLAIN SEQUENCE · DUNE SEQUENCE

N content (g/m²) — A, B
K content (g/m²) — C, D
P content (g/m²) — E, F

Foliage, Wood, Herbs, Litter

Soil-surface age (years)

PLAIN SEQUENCE

DUNE SEQUENCE

Fine roots   Rhizomes

Fine roots   Rhizomes

N concentration (mg/g)

40

30

20

10

0

A

B

K concentration (mg/g)

10

8

6

4

2

0

C

D

P concentration (mg/g)

2.0

1.5

1.0

0.5

0.0

E

F

12 20 28 100 200   12 20 28 100 200

12 20 28 100 200   12 20 28 100 200

Soil-surface age (years)

Fig 5

ORGANIC LAYER   **MINERAL LAYER**

PLAIN   DUNES   PLAIN   DUNES

Age (Years)
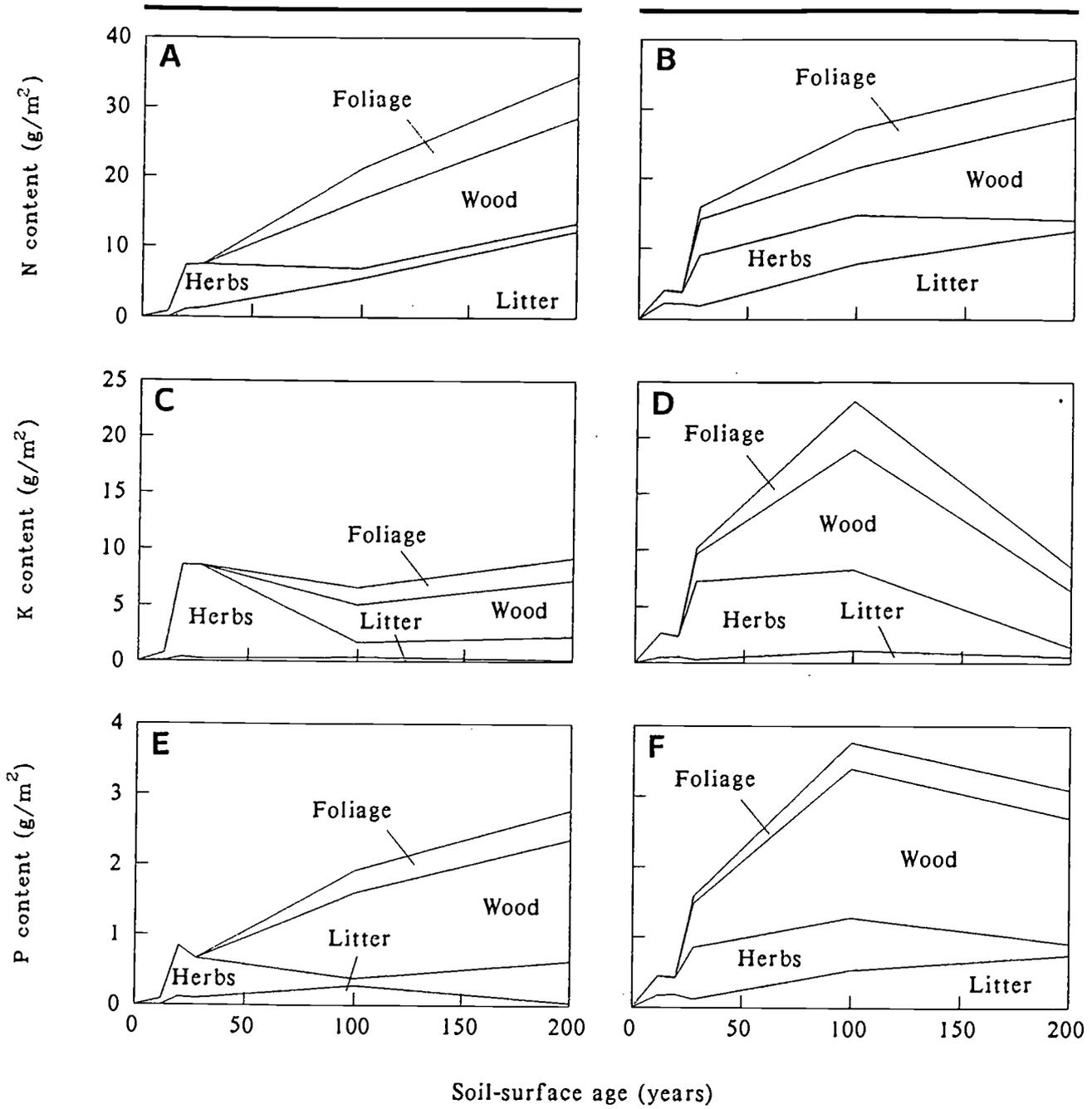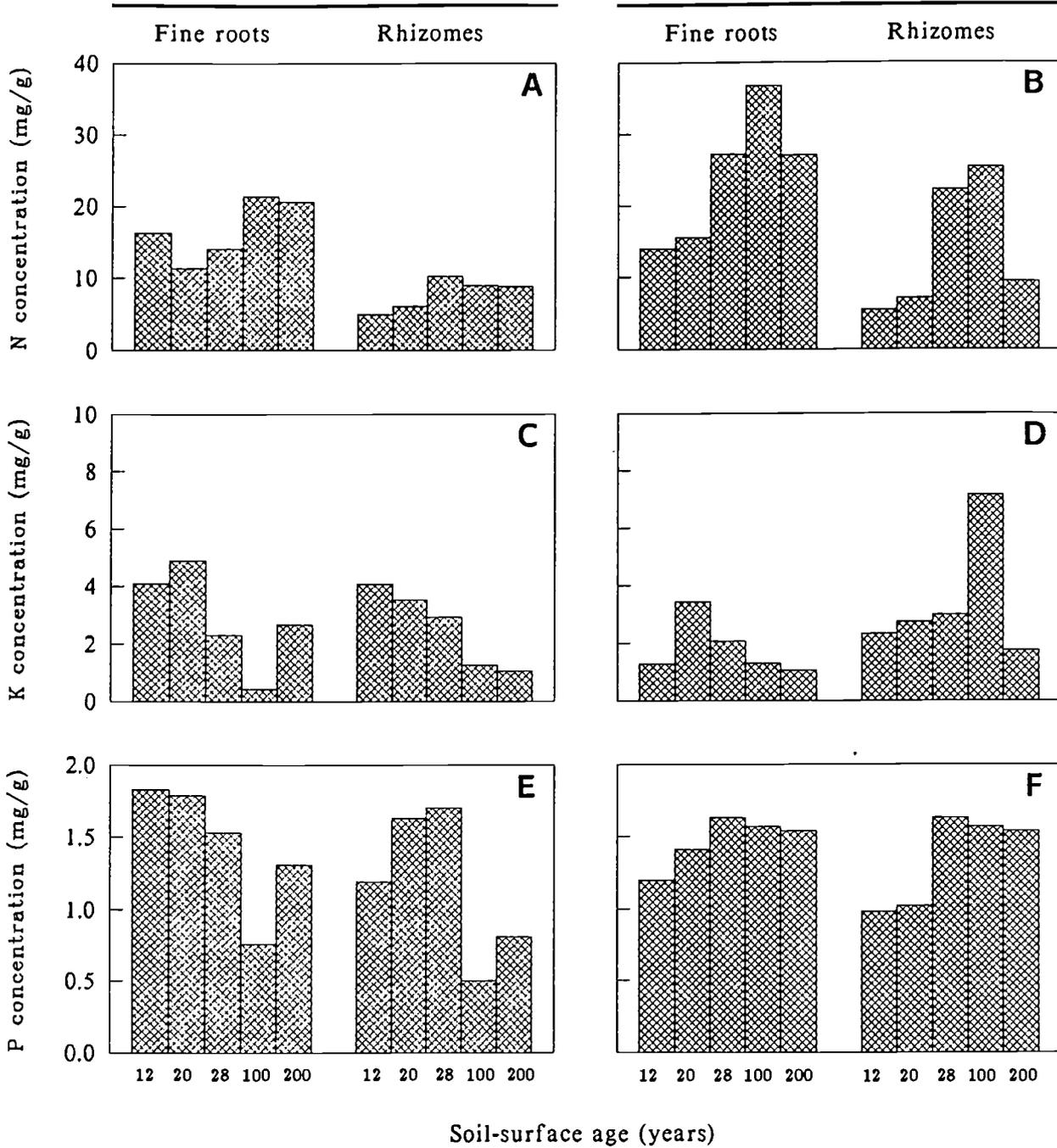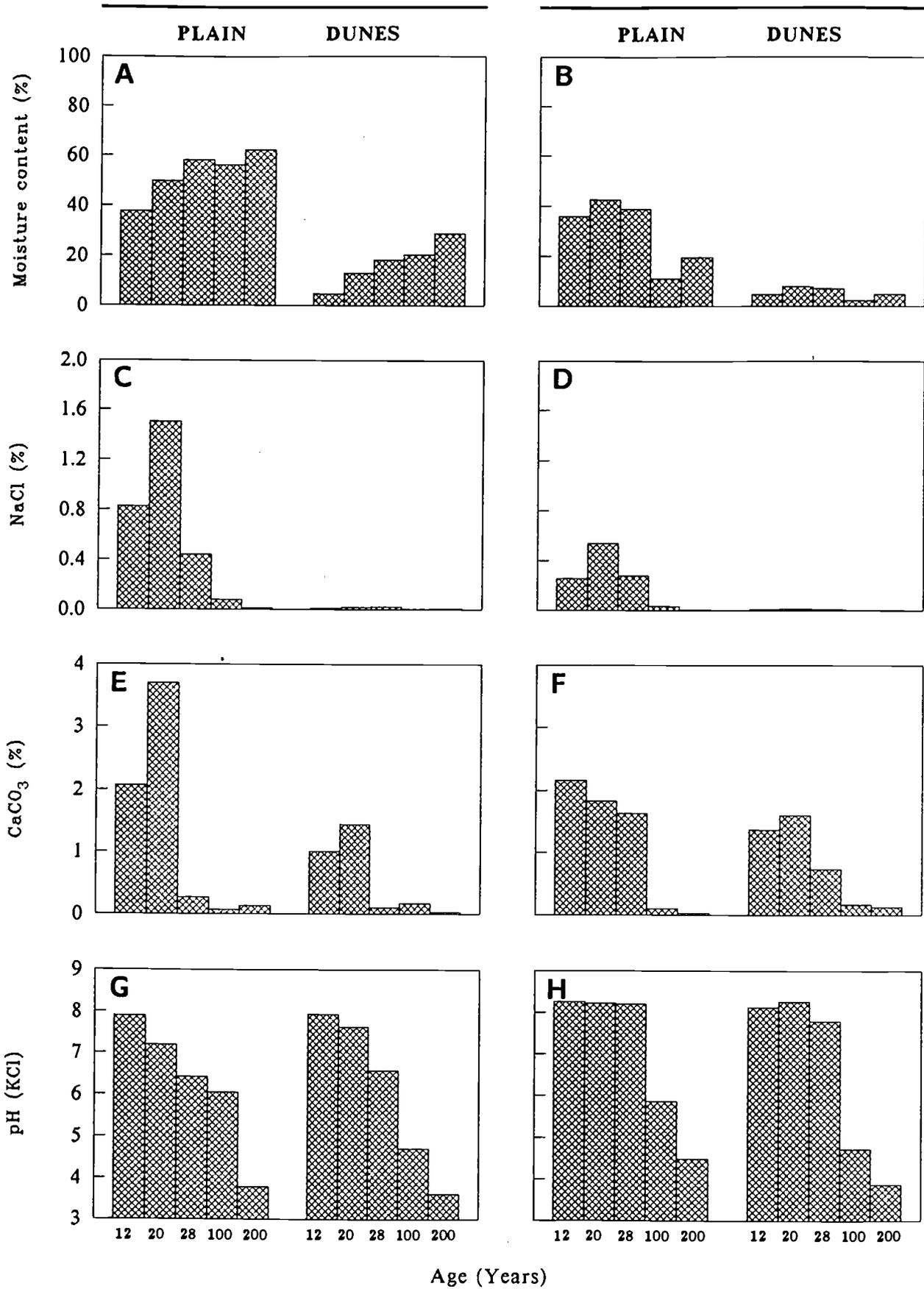
fig 6

ORGANIC LAYER

MINERAL LAYER

fig 7

PLAIN   DUNES

Fig.

PLAIN SEQUENCE

DUNE SEQUENCE

A Biomass Litter

SOM

B Biomass Litter

SOM

C Biomass Litter

SOM

D Litter Biomass

SOM

E Litter Biomass

SOM

F Biomass Litter

SOM

Soil-surface age (years)

Fig 10
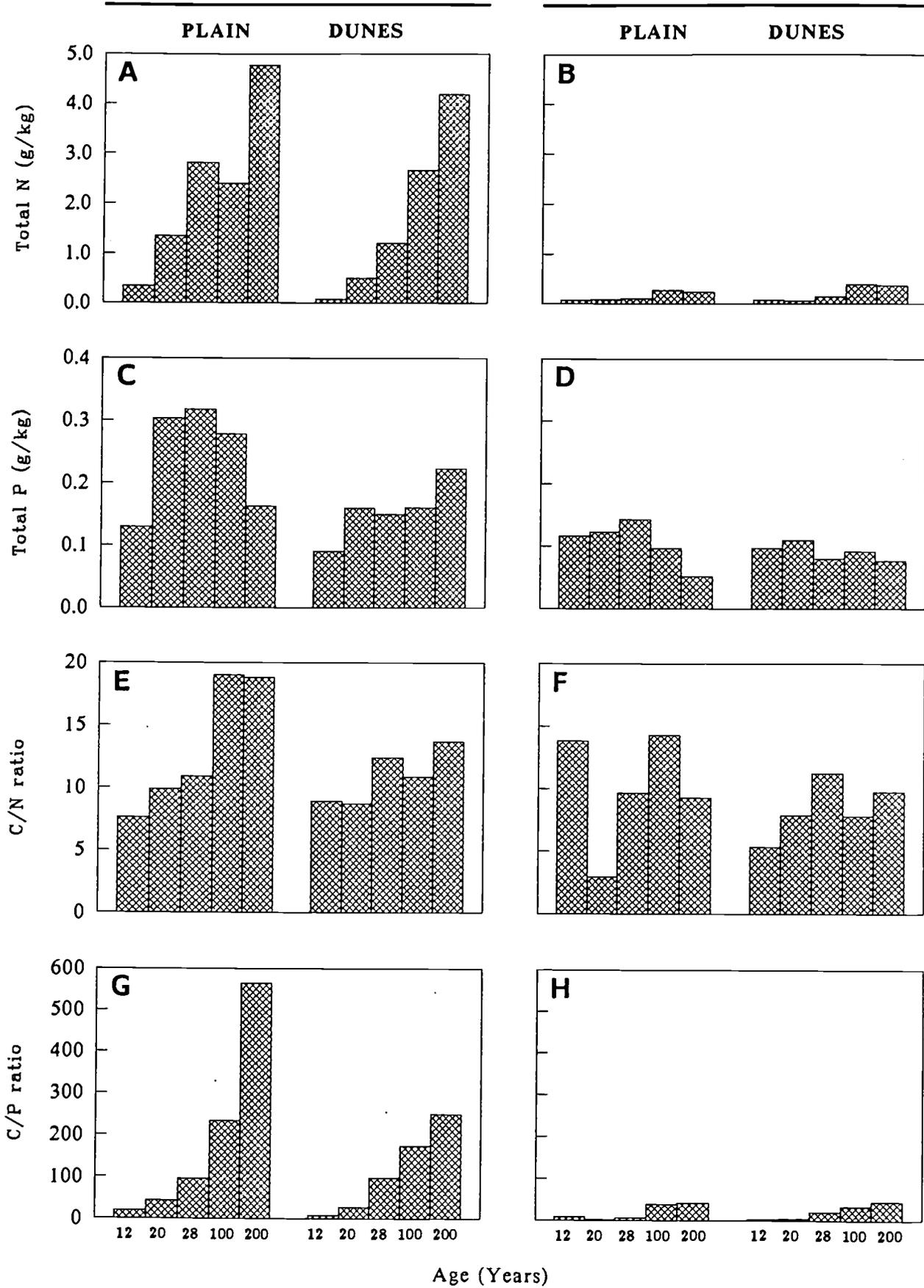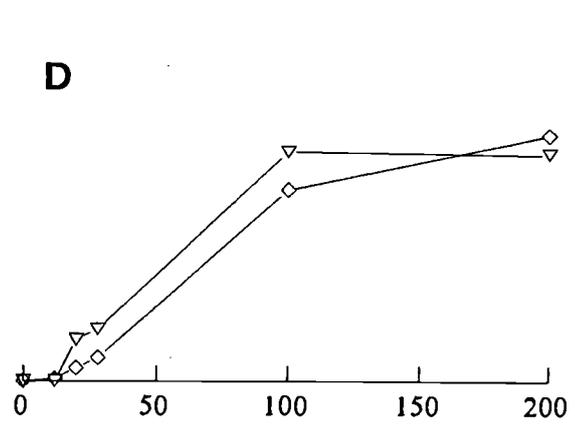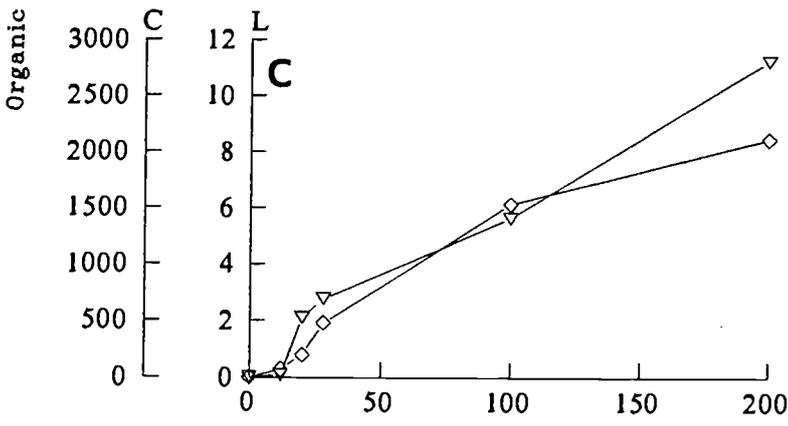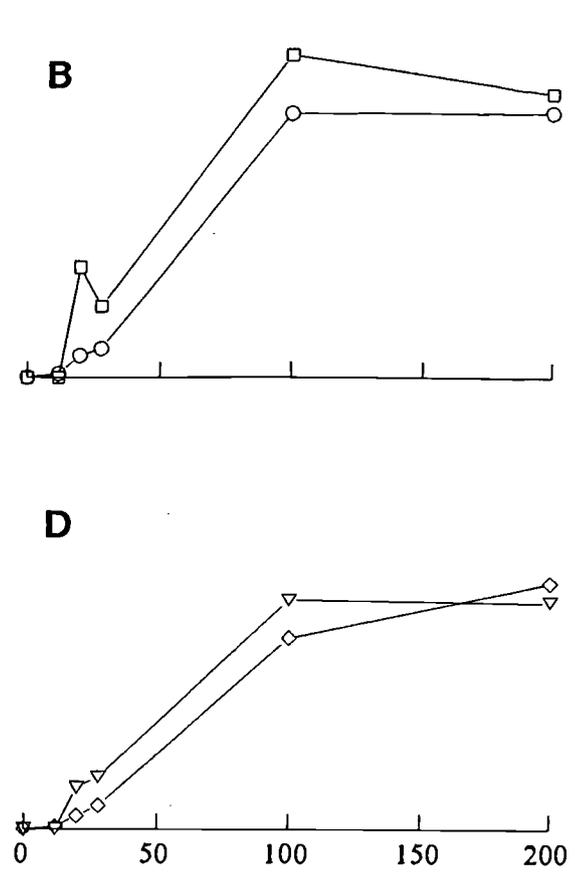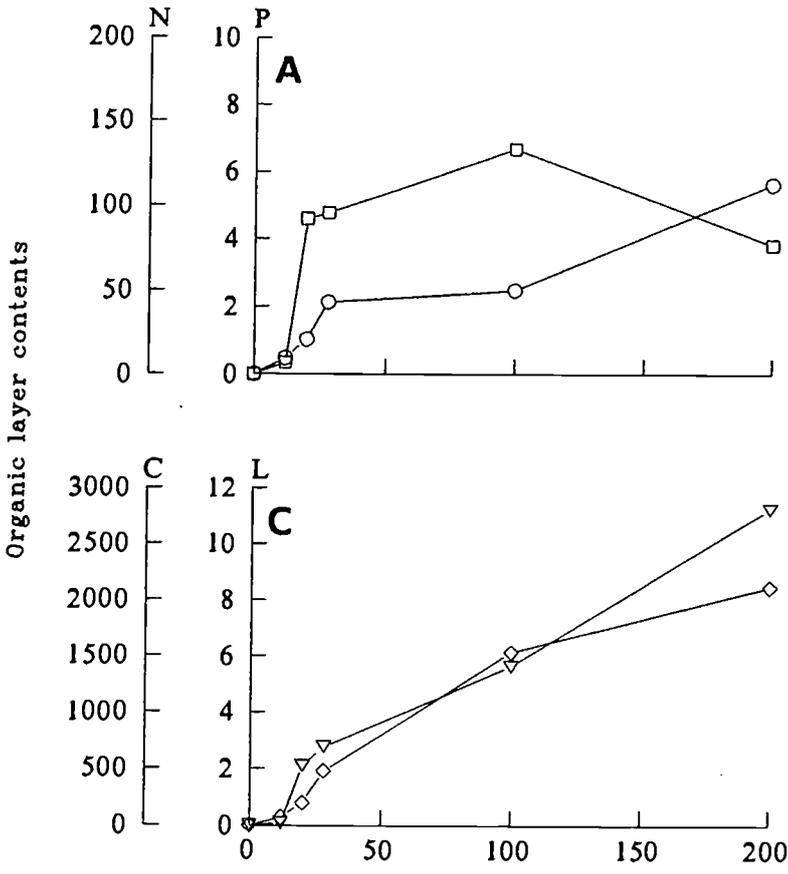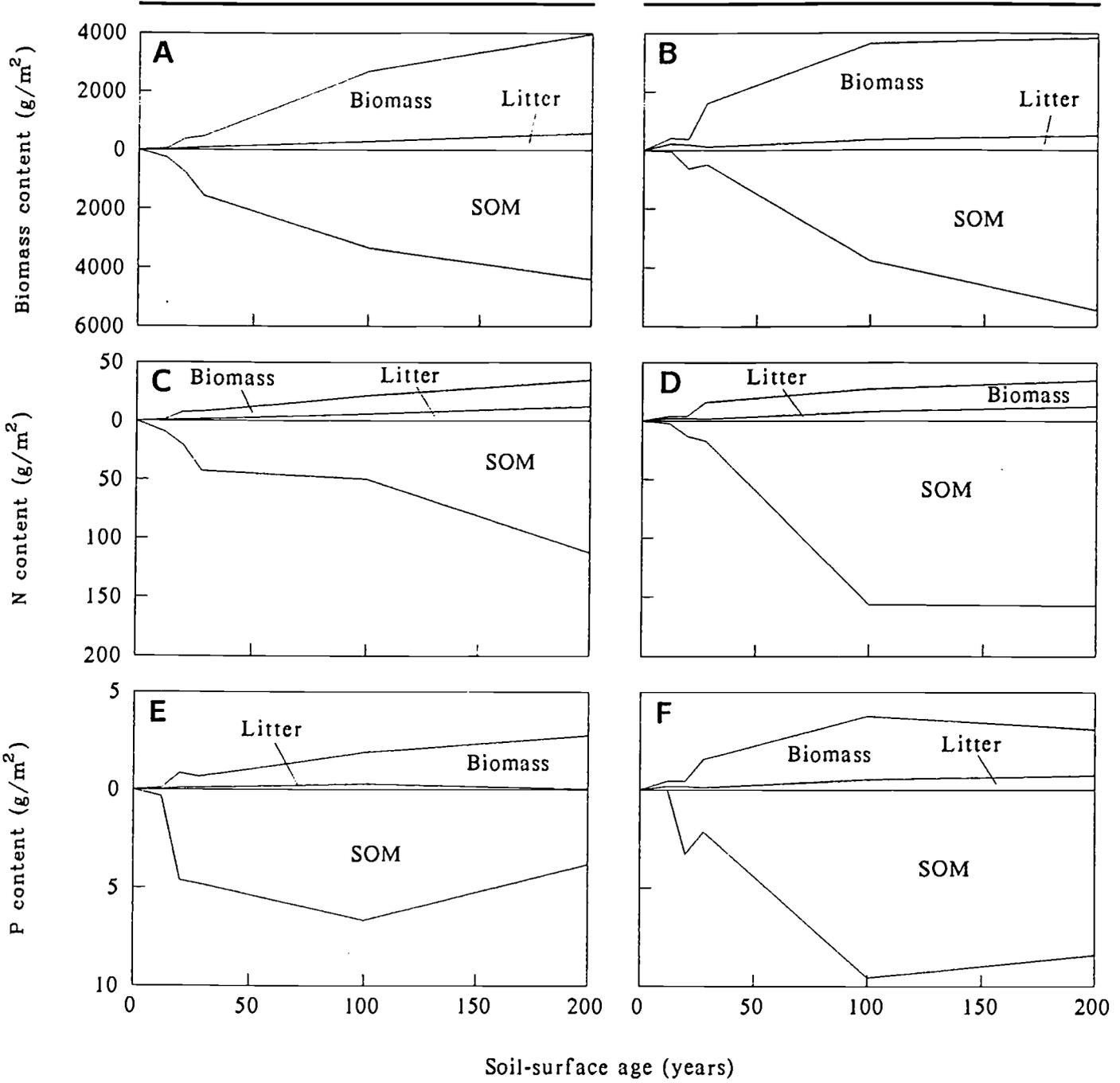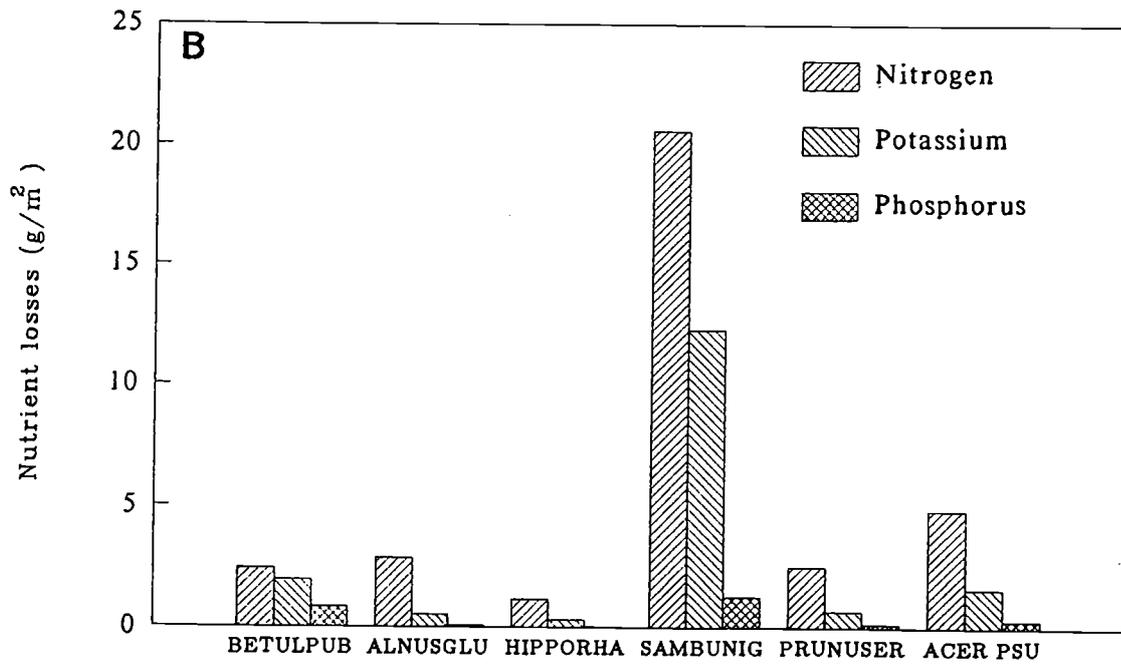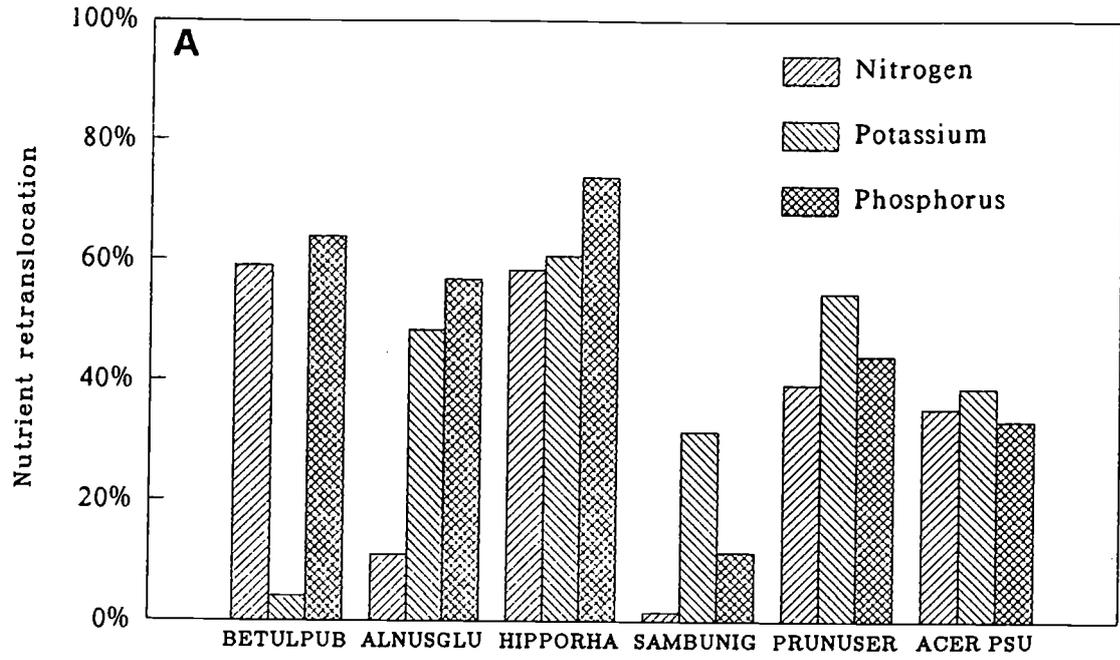
APPENDIX B

This appendix includes data and figures which were not used in the manuscript.

The figures B1-B4 include maps of the study sites in which the location of individual trees is marked. The lines mark the edges of the crowns of individual trees.

Figure B5 shows graphs in which a comparison between the predictions of the model and the data can be made.

Figure B6 includes the biomass per tree species on the study sites.

Figure B7 includes the percentage cover per tree species on the study sites.

Figure B8 shows graphs in which a comparison between the leaf biomass culculated with the regression lines and the leaf biomass calculated from the crown are multiplied with LAI and specific leaf area.
The graphs to the left were made using a LAI which was calculated with the data collected by myself. These data possibly include a overestimation of the leaf biomass. The graphs to the right were made using a LAI found in literature. These graphs show a overestimation of leaf biomass when using the regression lines for tree larger then approximately 10 cm DBH.

refr:
Hughes, M.K. 1971. Tree biocontent, net production and litter fall in a deciduous woodland. OIKOS 22:62-73.

Figures B9-B11 include the frequency distribution of tree height (left) and DBH (right) for tree species at the study sites.

Figure B13 include graphs which shows the relation between diameter (DBH) and tree height per tree species, using data from different study sites.

The tables 2-4 include data on the biomass and LAI per tree species per site. Table 2 gives the estimated biomass when the sites were a monoculture of a certain species.
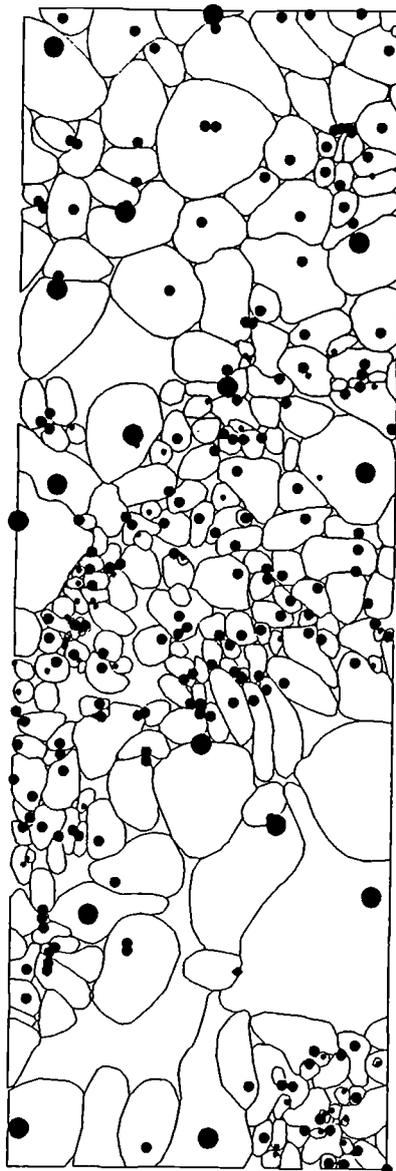
Figure 1 : Site 1; Het Johannesbos. Plot size : 10m²x30m². The dots represent the base of each individual tree. Legenda : ● *Betula pubescens*; ◆ *Hippophae rhamnoides*. The symbol size represents three diameter classes: small (0-2.5 cm φ), medium (2.5-10 cm φ) and large (10-50 cm φ). The lines mark the edges of the crowns of individual trees.

fig 81
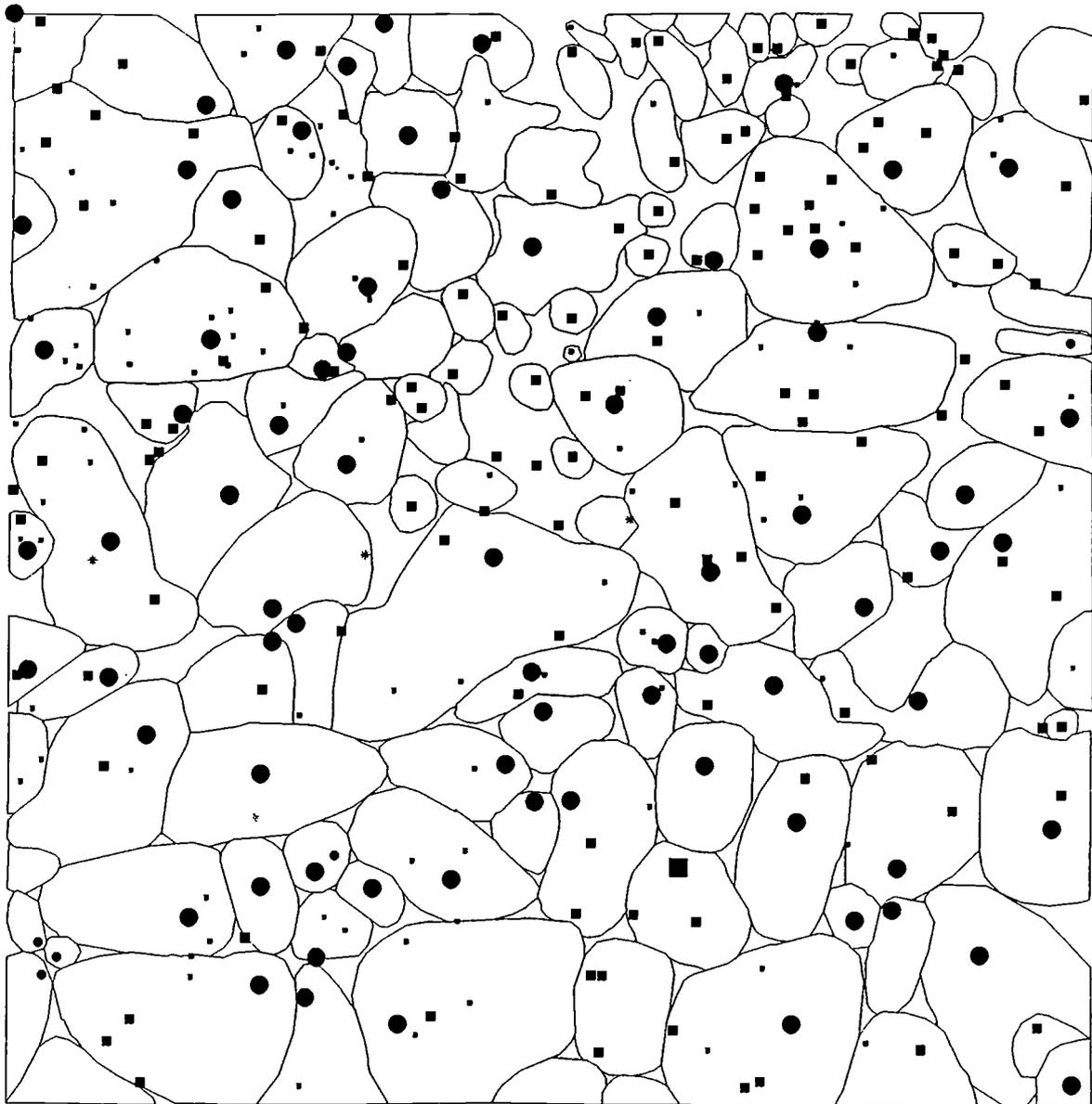
Figure 2 : Site 2; Het Berkenbos. Plot size : 30m²x30m². The dots represent the base of each individual tree. Legenda : ● *Betula pubescens*; ■ *Alnus glutinosa*, ✳ remaining species. The symbols represent three diameter classes: small (0-2.5 cm φ), medium (2.5-10 cm φ) and large (10-50 cm φ). The lines mark the edges of the crowns of individual trees.
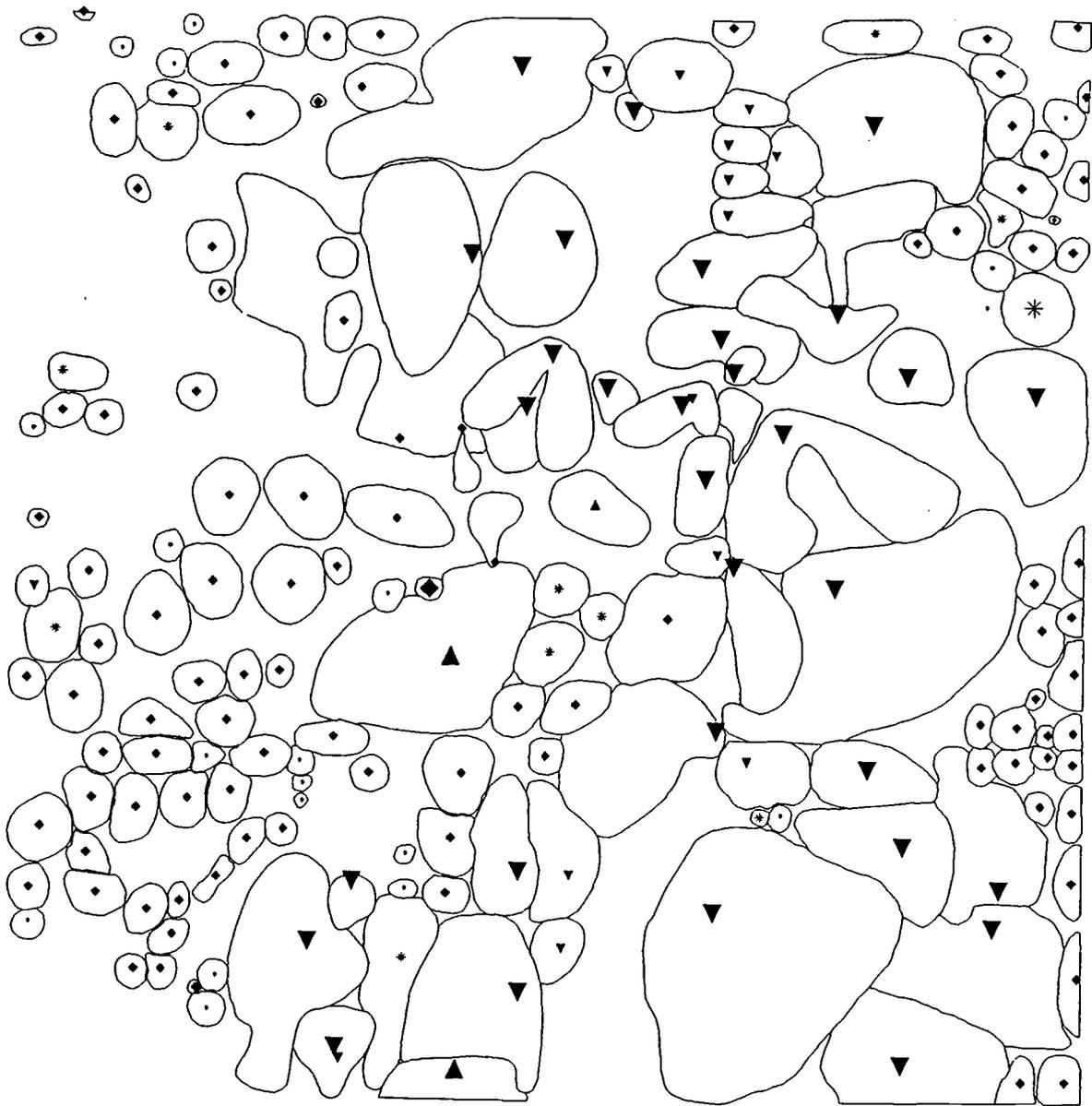
Figure 3 : Site 3; Het Kobbebos. Plot size : 30m²x30m². The dots represent the base of each individual tree. Legenda : ▼ *Sambucus nigra*, ◆ *Hippophae rhamnoides*, ▲ *Prunus serotina*, ✳ remaining species. The symbols represent three diameter classes: small (0-2.5 cm φ), medium (2.5-10 cm φ) and large (10-50 cm φ). The lines mark the edges of the crowns of individual trees. Only the crowns of trees in the upper layer are drawn.
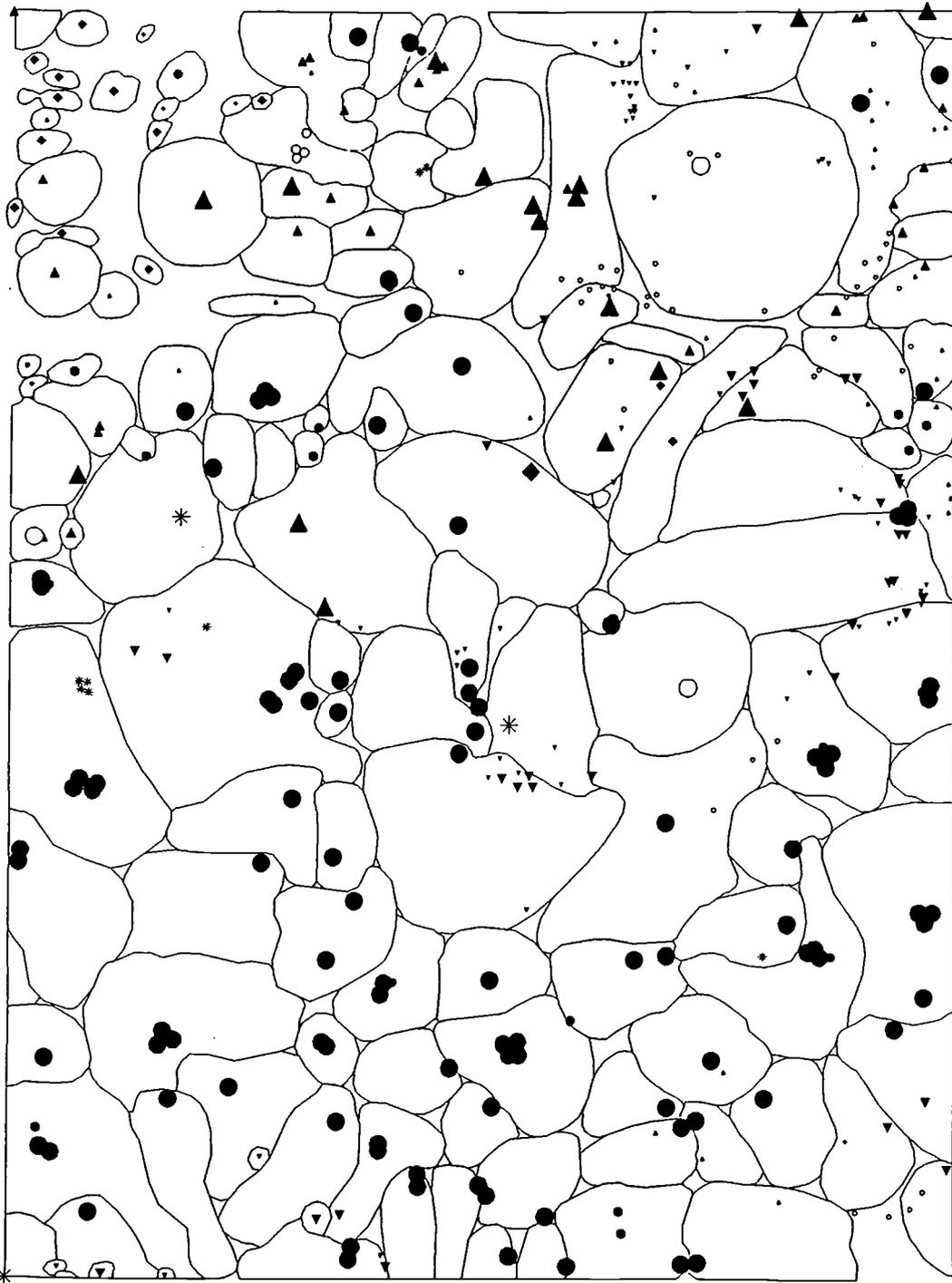
Figure 4 : Site 4; Het Kooibos. Plot size : 30m²x40m². The dots represent the base of each individual tree. Legenda : ● *Betula pubescens*, ▼ *Sambucus nigra*, ◆ *Hippohae rhamnoides*, ▲ *Prunus serotina*, O *Acer pseudoplatanus*, ✳ remaining species. The symbols represent three diameter classes: small (0-2.5 cm φ), medium (2.5-10 cm φ) and large (10-50 cm φ). The lines mark the edges of the crowns of individual trees. Only the crowns of trees in the upper layer are drawn.

Predictions :
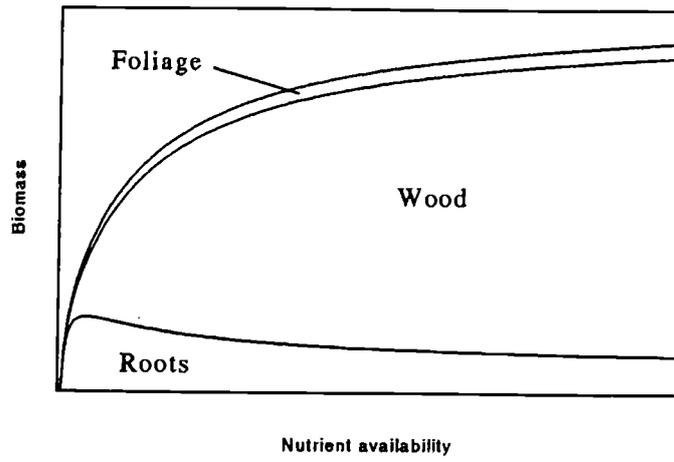
Biomass

Foliage

Wood

Roots

Nutrient availability

Biomass accumulation on the plain

Living biomass (g/m2)

5000
4000
3000
2000
1000
0

Foliage

Herbs

Wood

Roots

0   50   100   150   200

Age (Years)

Biomass accumulation on the dunes

Living biomass (g/m2)

5000
4000
3000
2000
1000
0

Foliage

Herbs

Wood

Roots

0   50   100   150   200

Age (Years)
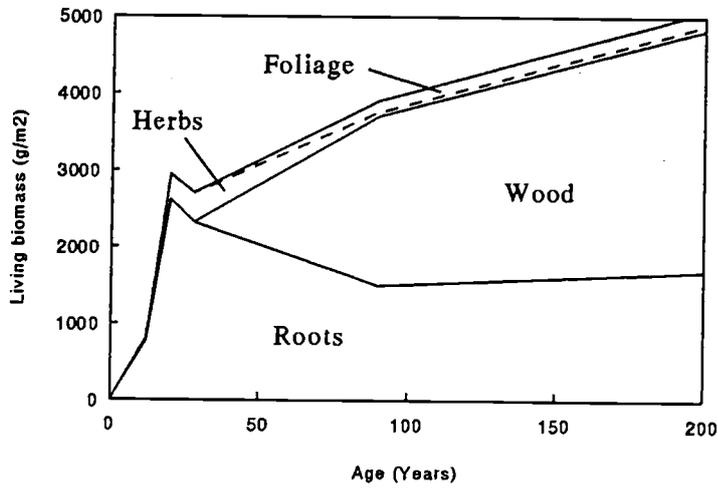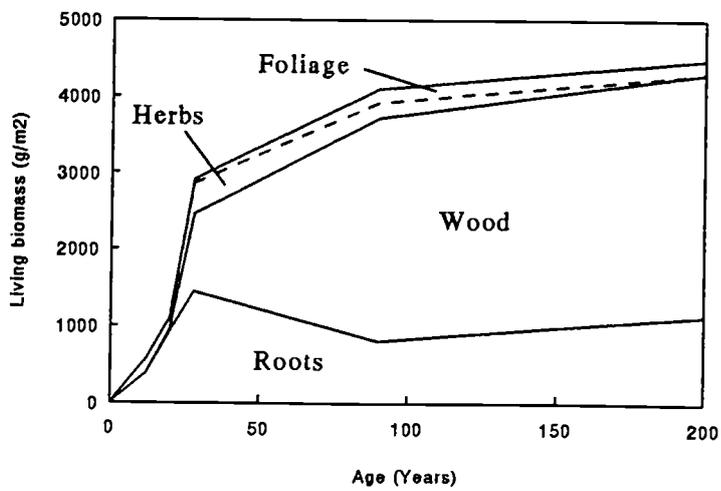
Distribution of above ground biomass phanerophytes

Biomass (kg/ha)

Johannesbos

Berkenbos

Kobbebos

Kooibos
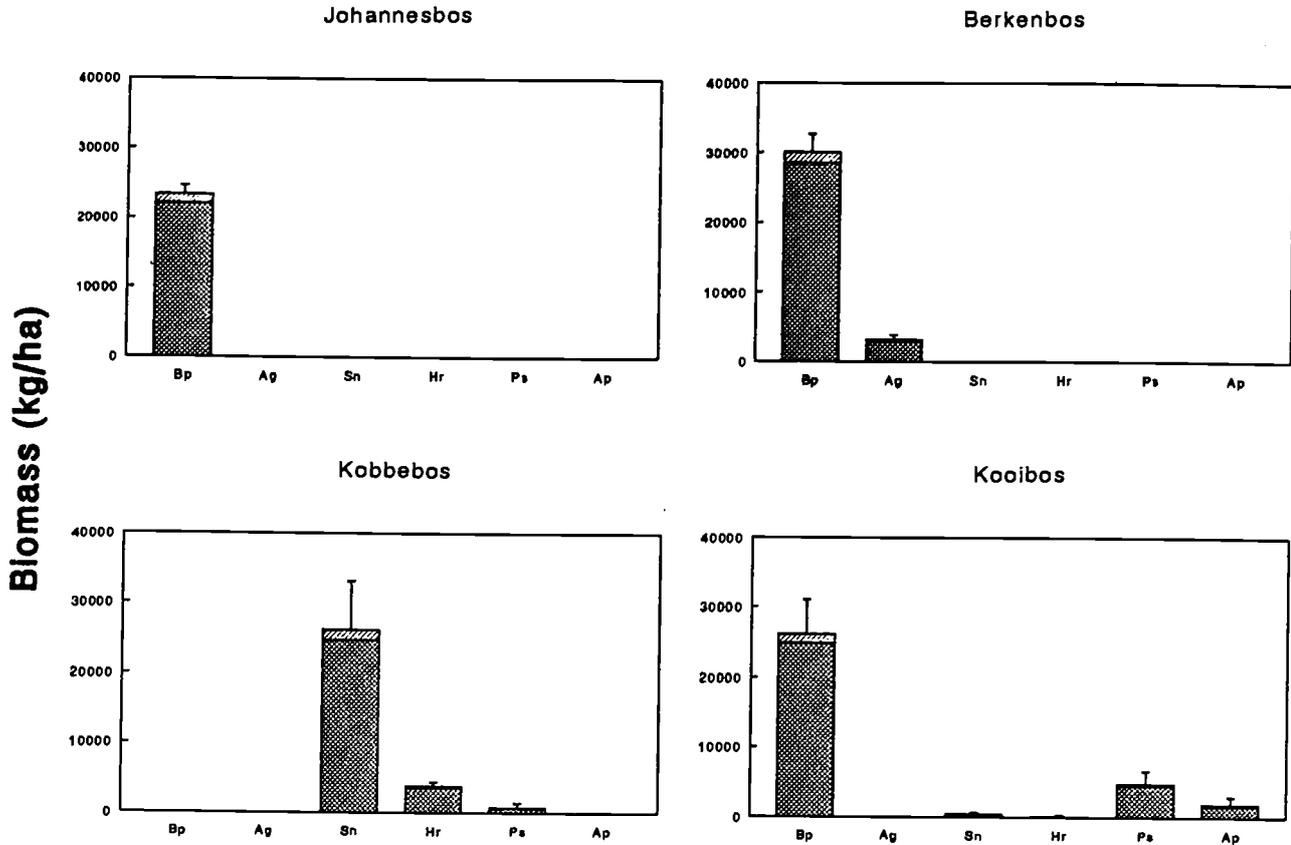
Biomass on the sites
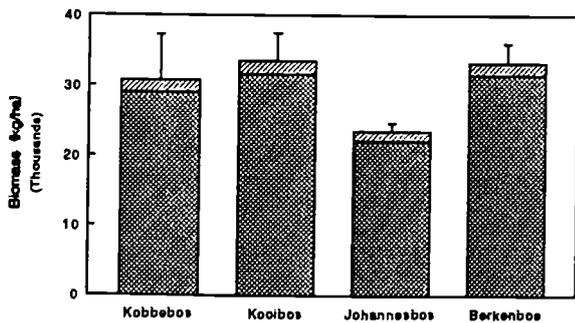
Legend :

Bp : Betula pubescens
Ag : Alnus glutinosa
Sn : Sambucus nigra
Hr : Hippophae rhamnoides
Ps : Prunus serotina
Ap : Acer pseudoplatanus

⬜ : Leafmass
⬛ : Stemmass
Error bar : Standard Error of total biomass

fig 80
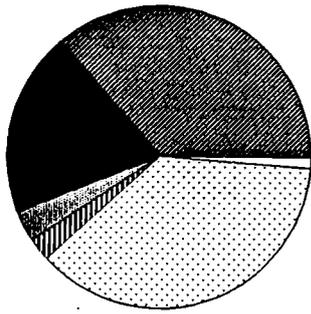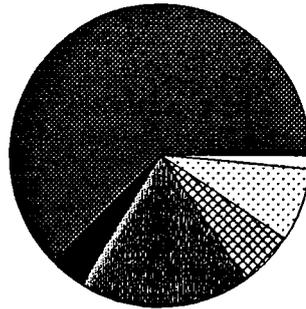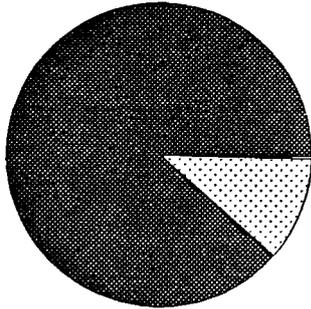
Het Kobbebos   Het Kooibos   Het Johannesbos   Het Berkebos

legend
- Betula pubescense
- Alnus glutinosa
- Sambucus nigra
- Hippophae rham.
- Crataegus monogyna
- Prunus serotina
- Acer pseudoplatanus.
- Rubus caesius
- Open
- Rest
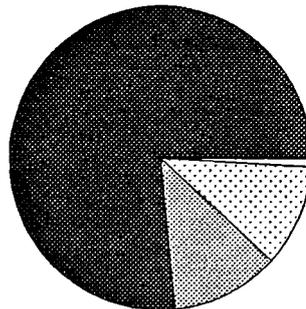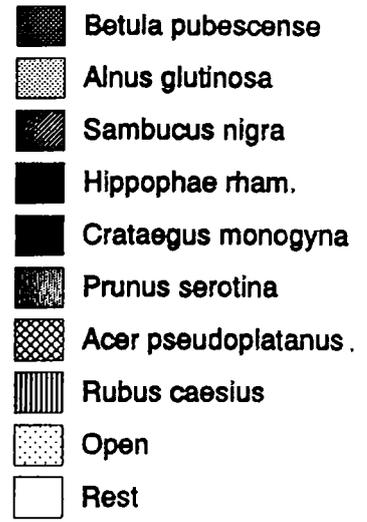
Percentage cover of the tree species at the study sites.

OWN LAI USED

LAI FROM LITERATURE

BETULA PUBESCENS

LAI = 3.16

FROM THE BERKENBOS

LAI = 1.55
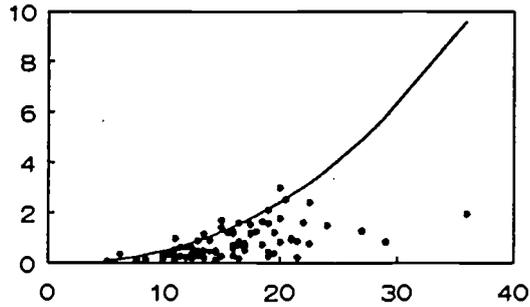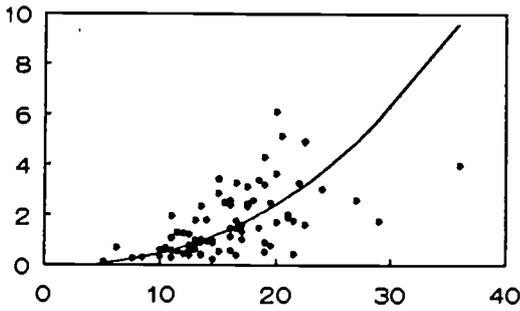
ALNUS GLUTINOSA

LAI = 1.97

FROM THE BERKENBOS

LAI = 2.08
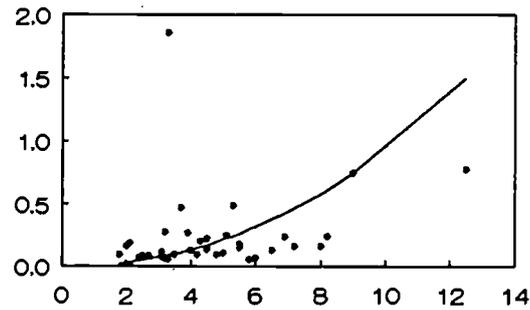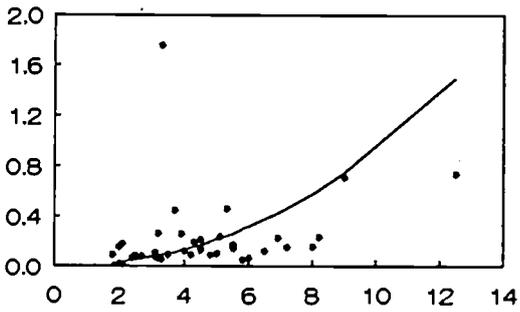
BETULA PUBESCENS

LAI = 2.52

FROM THE JOHANNESBOS

LAI = 1.55

DBH (CM)

Leaf biomass per individual (kg dry weight)
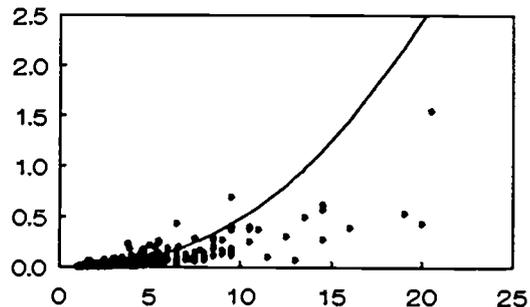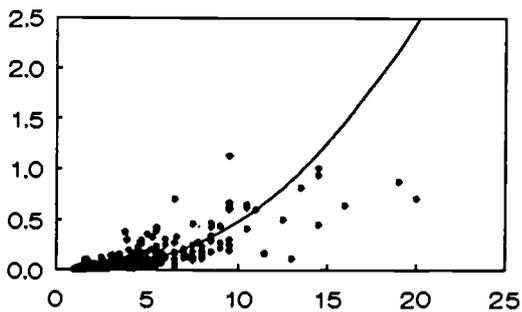
Lines   : Leaf biomass calculated with
                regression lines
Points   : Leaf biomass calculated with
                crown area and LAI

fig 88

Het Johannesbos

Betula pubescens
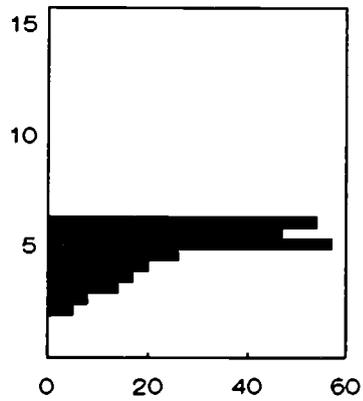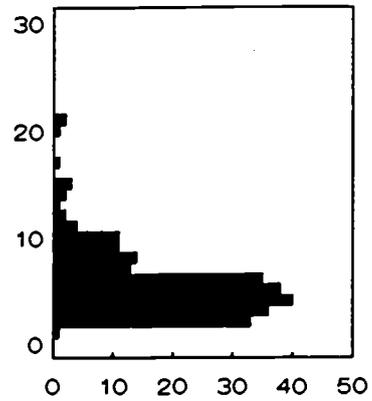
Betula pubescens

Het Berkebos

Betula pubescens
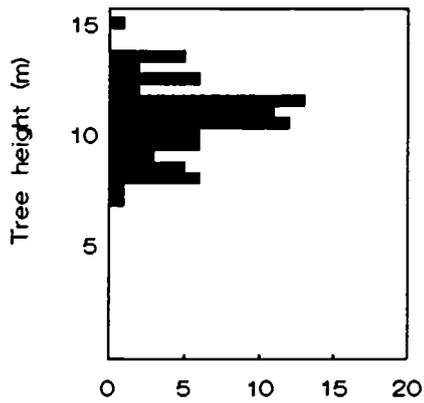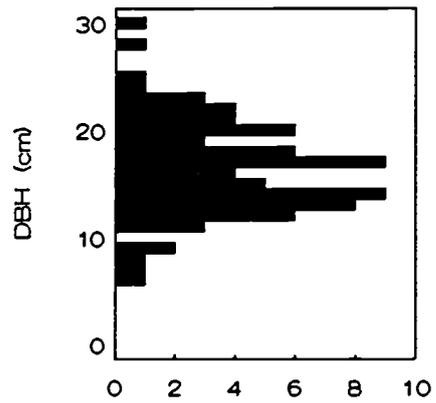
Betula pubescens

Alnus glutinosa

Alnus glutinosa

Tree height (m)

DBH (cm)

Number of trees

Het Kobbebos

Sambucus nigra

Sambucus nigra

Hippophae rhamnoides

Hippophae rhamnoides

Tree height (m)
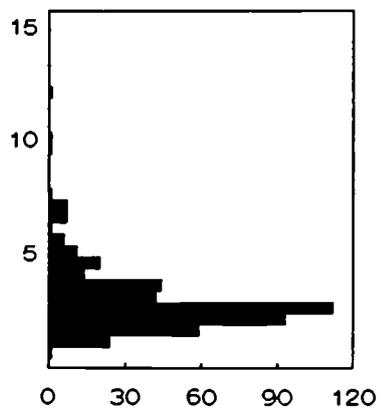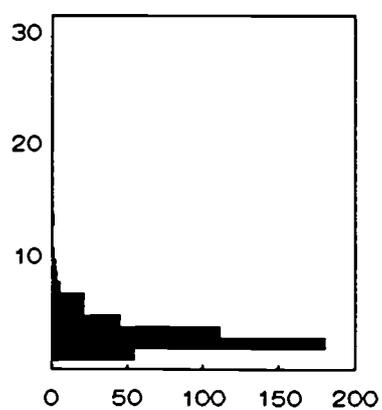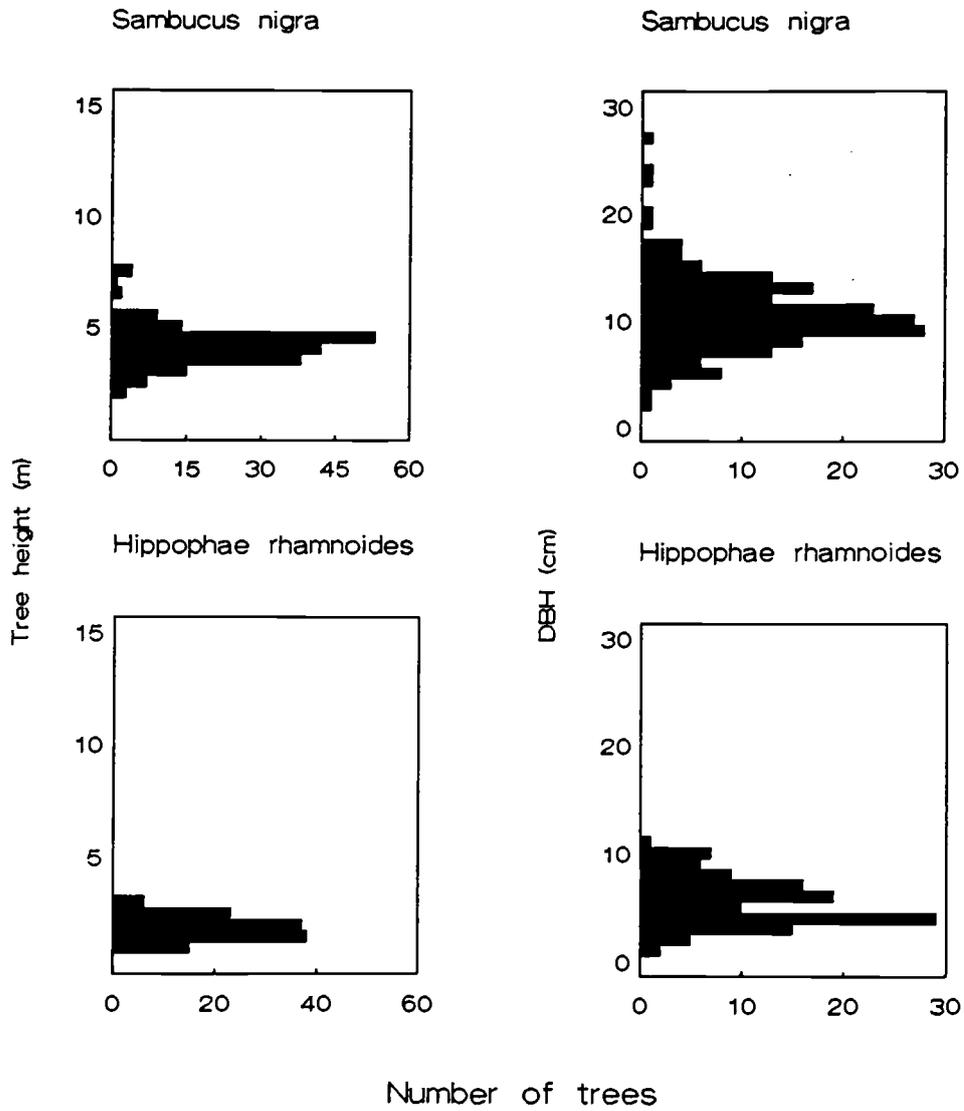
DBH (cm)

Number of trees

Het Kooibos

Betula pubescens

Betula pubescens

Hippophae rhamnoides

Hippophae rhamnoides

Tree height (m)
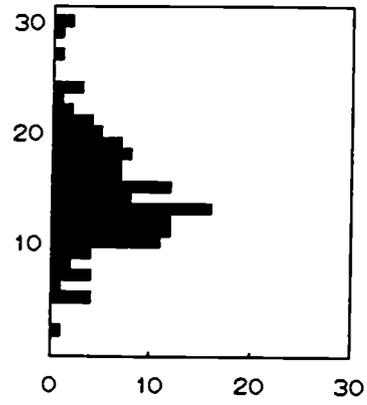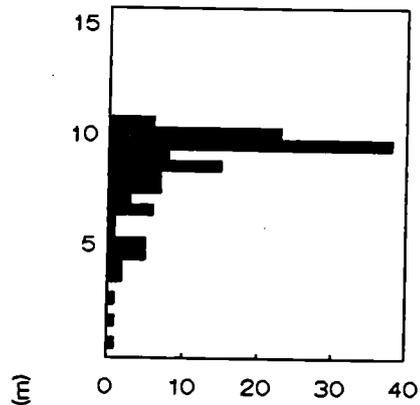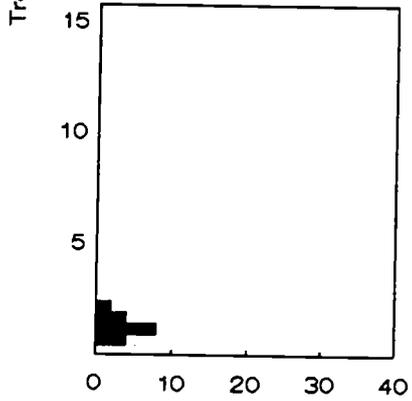
DBH (cm)
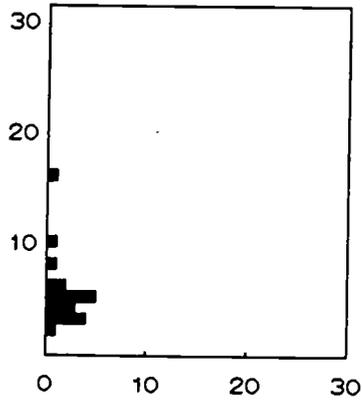
Number of trees

Het Kooibos

Prunus serotina
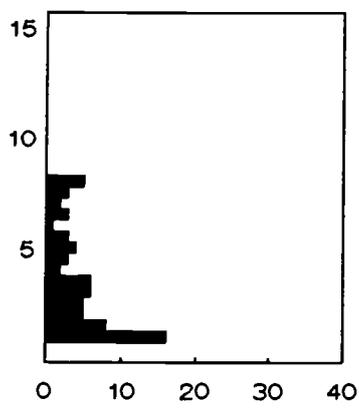
Prunus serotina
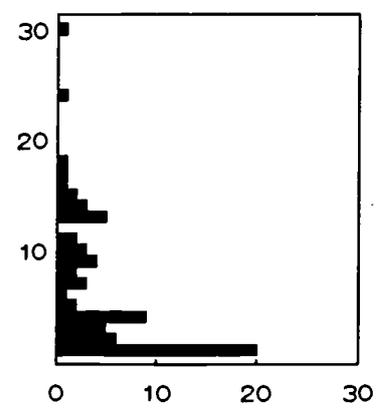
Acer pseudoplatanus
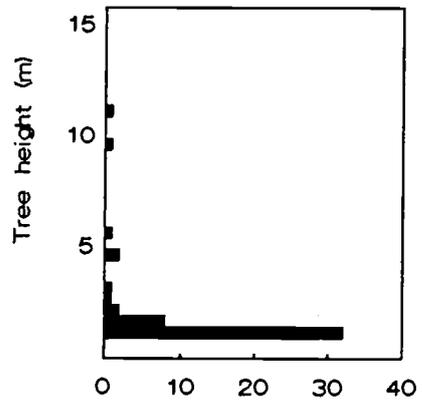
Acer pseudoplatanus
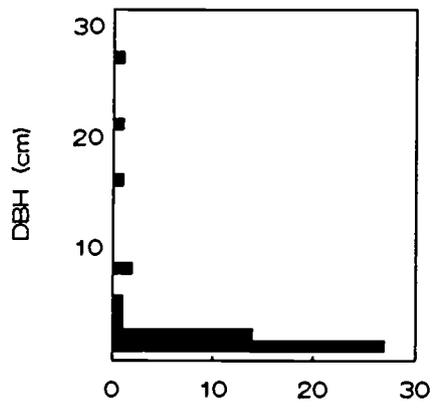
Sambucus nigra
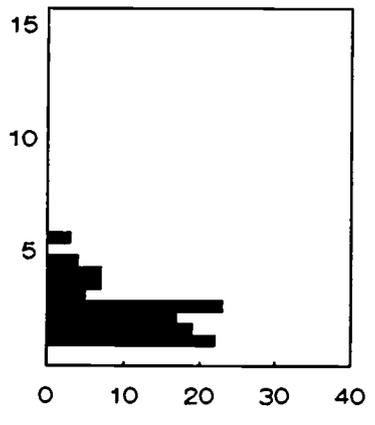
Sambucus nigra

Number of trees

Tree height (m)

DBH (cm)
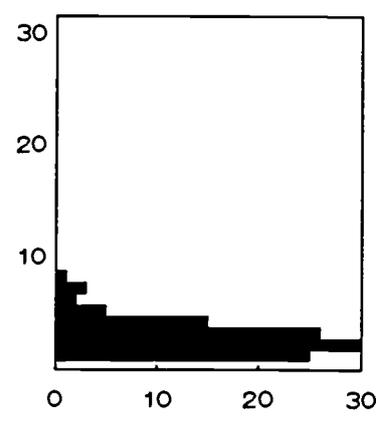
Relatie diameter - hoogte

Betula pubescens

□ Berkebos + Johannes ◇ Kooibos

Alnus glutinosa   **Berkenbos**

Tree height

Diameter
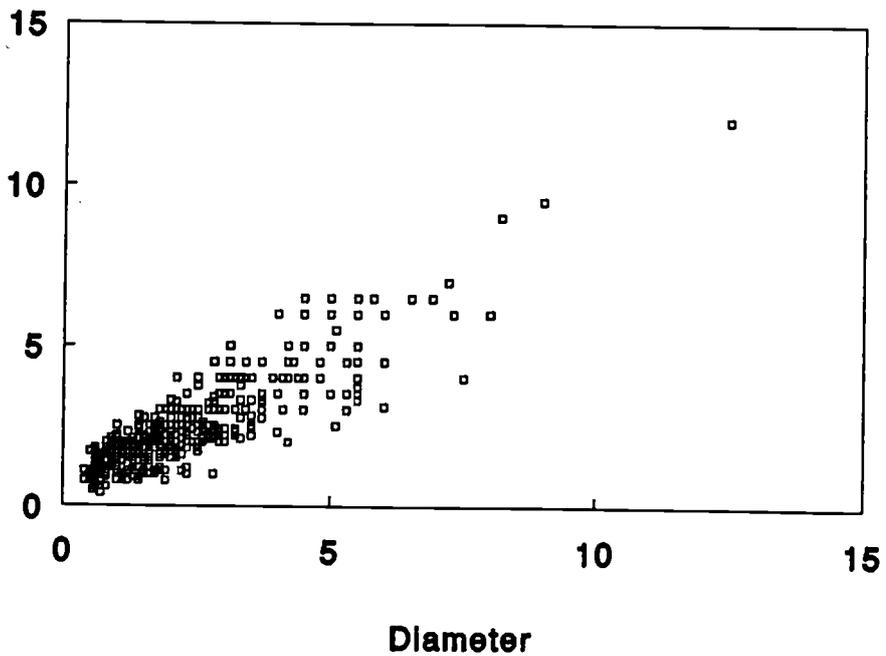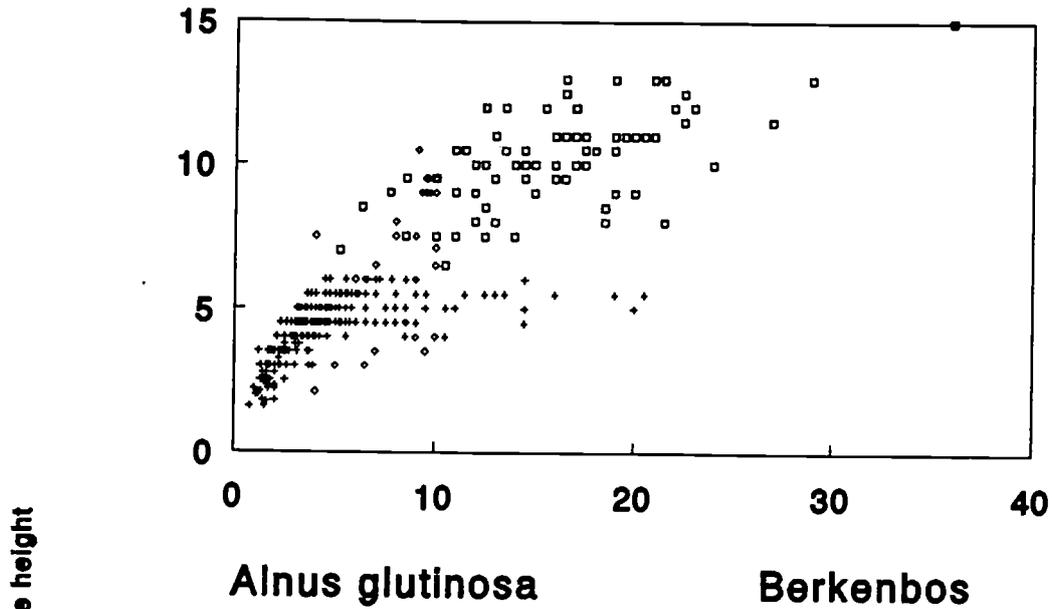
Table 2. Biomass distribution

Total aboveground biomass per species (kg/ha)

species :	Kobbebos	Kooibos	Johannesbos	Berkenbos
Betula pubescens		26212	23388	30021
Alnus Glutinosa				3238
Sambucus nigra	26201	444		
Hippophae rhamnoides	3742	144	74	
Prunus serotina	770	4800		
Acer psuedoplatanus		1870		
Totaal :	30713	33470	23462	33259

Total leaf biomass per species (kg/ha)

	Kobbebos	Kooibos	Johannesbos	Berkenbos
Betula pubescens		1321	1357	1475
Alnus Glutinosa				307
Sambucus nigra	1494	51		
Hippophae rhamnoides				
Prunus serotina	52	316		
Acer psuedoplatanus		185		
Totaal :	1546	1873	1357	1782

Total stem biomass per species (kg/ha)

	Kobbebos	Kooibos	Johannesbos	Berkenbos
Betula pubescens		24891	22031	28546
Alnus Glutinosa				2931
Sambucus nigra	24707	393		
Hippophae rhamnoides				
Prunus serotina	718	4484		
Acer psuedoplatanus		1685		
Totaal :	25425	31453	22031	31477

Total biomassa on the sites
(including estimated Hippophae values for leaf and stem biomass.)

	Kobbebos	Kooibos	Johannesbos	Berkenbos
Total	30713	33470	23462	33259
leaf	1733	1880	1364	1782
Stem	28979	31589	22099	31477

Table 2

Table 3. Potential biomass per species

Total aboveground biomass per species in monoculture (kg/ha)

	Kobbebos	Kooibos	Johannesbos	Berkenbos
Betula pubescens		41762	26437	39131
Alnus Glutinosa				8658
Sambucus nigra	73548	56720		
Hippophae rhamnoides	19315	16702	17903	
Prunus serotina	24265	26307		
Acer psuedoplatanus		30885		

Total leaf biomass per species in monoculture (kg/ha)

	Kobbebos	Kooibos	Johannesbos	Berkenbos
Betula pubescens		2104	1534	1922
Alnus Glutinosa				821
Sambucus nigra	4194	6539		
Hippophae rhamnoides				
Prunus serotina	1649	1732		
Acer psuedoplatanus		3057		

Total stem biomass per species in monoculture (kg/ha)

	Kobbebos	Kooibos	Johannesbos	Berkenbos
Betula pubescens		39658	24903	37209
Alnus Glutinosa				7837
Sambucus nigra	69355	50192		
Hippophae rhamnoides				
Prunus serotina	22619	24575		
Acer psuedoplatanus		27828		

Jatie 3

Table 4. Leaf Area Index (LAI) of the species on the sites.

LAI (m² leaf / m² occupied by species.)

	Kobbebos	Kooibos	Johanbos	Berkenbos	SLA
Betula pubescens		3.46	2.52	3.16	164
Alnus Glutinosa				1.97	240
Sambucus nigra	5.46	2.31			130
Hippophae rhamnoides					
Prunus serotina	4.32	4.54			262
Acer psuedoplatanus		5.40			177

Table 4